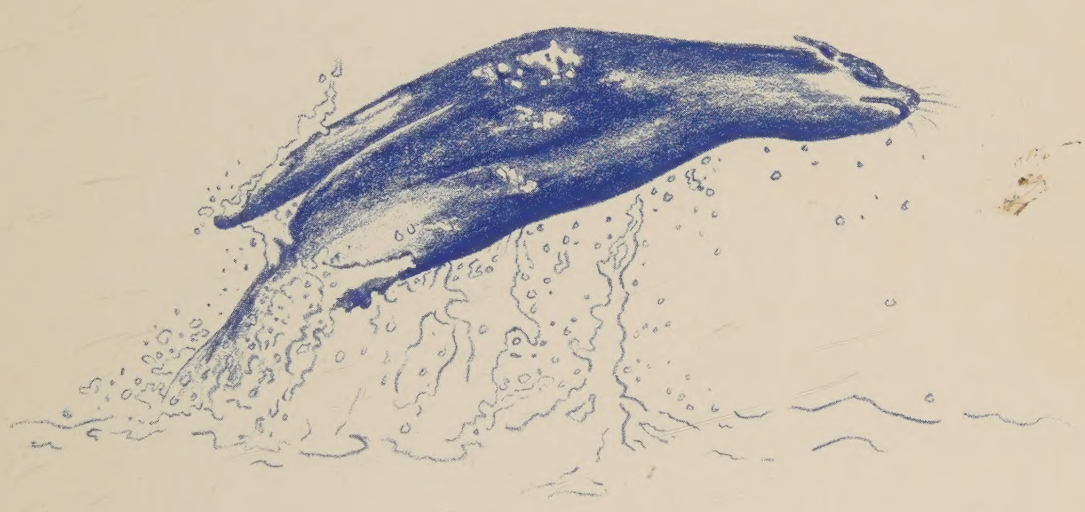
LIBRARY
NOV 1987
Service
Honolulu, Hawaii

NOAA Technical Report NMFS 51 June 1987

Status, Biology, and Ecology of Fur Seals

Proceedings of an International Symposium and Workshop Cambridge, England, 23-27 April 1984

John P. Croxall
Roger L. Gentry (*editors*)



U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

NOAA TECHNICAL REPORT NMFS

The major responsibilities of the National Marine Fisheries Service (NMFS) are to monitor and assess the abundance and geographic distribution of fishery resources, to understand and predict fluctuations in the quantity and distribution of these resources, and to establish levels for their optimum use. NMFS is also charged with the development and implementation of policies for managing national fishing grounds, development and enforcement of domestic fisheries regulations, surveillance of foreign fishing off United States coastal waters, and the development and enforcement of international fishery agreements and policies. NMFS also assists the fishing industry through marketing service and economic analysis programs, and mortgage insurance and vessel construction subsidies. It collects, analyzes, and publishes statistics on various phases of the industry.

The NOAA Technical Report NMFS series was established in 1983 to replace two subcategories of the Technical Reports series: "Special Scientific Report—Fisheries" and "Circular." The series contains the following types of reports: Scientific investigations that document long-term continuing programs of NMFS; intensive scientific reports on studies of restricted scope; papers on applied fishery problems; technical reports of general interest intended to aid conservation and management; reports that review in considerable detail and at a high technical level certain broad areas of research; and technical papers originating in economics studies and from management investigations. Since this is a formal series, all submitted papers receive peer review and those accepted receive professional editing before publication.

Copies of NOAA Technical Reports NMFS are available free in limited numbers to governmental agencies, both Federal and State. They are also available in exchange for other scientific and technical publications in the marine sciences. Individual copies may be obtained from: U.S. Department of Commerce, National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22161. Although the contents have not been copyrighted and may be reprinted entirely, reference to source is appreciated.

13. Guidelines for reducing porpoise mortality in tuna purse seining, by James M. Coe, David B. Holts, and Richard W. Butler. September 1984, 16 p.

14. Synopsis of biological data on shortnose sturgeon, *Acipenser brevirostrum* LeSueur 1818, by Michael J. Dadswell, Bruce D. Taubert, Thomas S. Squiers, Donald Marchette, and Jack Buckley. October 1984, 45 p.

15. Chaetognatha of the Caribbean sea and adjacent areas, by Harding B. Michel. October 1984, 33 p.

16. Proceedings of the Ninth and Tenth U.S.-Japan Meetings on Aquaculture, by Carl J. Sindermann (editor). November 1984, 92 p.

17. Identification and estimation of size from the beaks of 18 species of cephalopods from the Pacific Ocean, by Gary A. Wolff. November 1984, 50 p.

18. A temporal and spatial study of invertebrate communities associated with hard-bottom habitats in the South Atlantic Bight, by E. L. Wenner, P. Hinde, D. M. Knott, and R. F. Van Dolah. November 1984, 104 p.

19. Synopsis of biological data on spottail pinfish, *Diplodus holbrooki* (Pisces: Sparidae), by George H. Darcy. January 1985, 11 p.

20. Ichthyoplankton of the Continental Shelf near Kodiak Island, Alaska, by Arthur W. Kendall, Jr., and Jean R. Dunn. January 1985, 89 p.

21. Annotated bibliography on hypoxia and its effects on marine life, with emphasis on the Gulf of Mexico, by Maurice L. Renaud. February 1985, 9 p.

22. Congrid eels of the eastern Pacific and key to their Leptocephali, by Solomon N. Raju. February 1985, 19 p.

23. Synopsis of biological data on the pinfish, *Lagodon rhomboides* (Pisces:Sparidae), by George H. Darcy. February 1985, 32 p.

24. Temperature conditions in the cold pool 1977-81: A comparison between southern New England and New York transects, by Steven K. Cook. February 1985, 22 p.

25. Parasitology and pathology of marine organisms of the world ocean, by William J. Hargis, Jr. (editor). March 1985, 135 p.

26. Synopsis of biological data on the sand perch, *Diplectrum formosum* (Pisces: Serranidae), by George H. Darcy. March 1985, 21 p.

27. Proceedings of the Eleventh U.S.-Japan Meeting on Aquaculture, Salmon Enhancement, Tokyo, Japan, October 19-20, 1982, by Carl J. Sindermann (editor). March 1985, 102 p.

28. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific, by William F. Perrin, Michael D. Scott, G. Jay Walker, and Virginia L. Cass. March 1985, 28 p.

29. Prevalence, intensity, longevity, and persistence of *Anisakis* sp. larvae and *Lacistorhynchus tenuis* metacestodes in San Francisco striped bass, by Mike Moser, Judy A. Sakanari, Carol A. Reilly, and Jeannette Whipple. April 1985, 4 p.

30. Synopsis of biological data on the pink shrimp, *Pandalus borealis* Krøyer, 1838, by Sandra E. Shumway, Herbert C. Perkins, Daniel F. Schick, and Alden P. Stickney. May 1985, 57 p.

NMFS Honolulu Library
00000000004741

31. Shark catches from selected fisheries off the U.S. east coast, by Emory D. Anderson, John G. Casey, John J. Hoey, and W. N. Witzell. July 1985, 22 p.

32. Nutrient Distributions for Georges Bank and adjacent waters in 1979, by A. F. J. Draxler, A. Matte, R. Waldhauer, and J. E. O'Reilly. July 1985, 34 p.

33. Marine flora and fauna of the Northeastern United States. Echinodermata: Echinoidea, by D. Keith Serafy and F. Julian Fell. September 1985, 27 p.

34. Additions to a revision of the shark genus *Carcharhinus*: Synonymy of *Aprionodon* and *Hypoprion*, and description of a new species of *Carcharhinus* (Carcharhinidae), by J. A. F. Garrick. November 1985, 26 p.

35. Synoptic review of the literature on the Southern oyster drill *Thais haemastoma floridana*, by Philip A. Butler. November 1985, 9 p.

36. An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*, by Reuben Lasker (editor). December 1985, 99 p.

37. A histopathologic evaluation of gross lesions excised from commercially important North Atlantic marine fishes, by Robert A. Murchelano, Linda Despres-Patanjo, and John Ziskowski. March 1986, 14 p.

38. Fishery atlas of the northwestern Hawaiian Islands, by Richard N. Uchida and James H. Uchiyama (editors). September 1986, 142 p.

39. Survey of fish protective facilities at water withdrawal sites on the Snake and Columbia Rivers, by George A. Swan, Tommy G. Withrow, and Donn L. Park. April 1986, 34 p.

40. Potential impact of ocean thermal energy conversion (OTEC) on fisheries, by Edward P. Myers, Donald E. Hoss, Walter M. Matsumoto, David S. Peters, Michael P. Seki, Richard N. Uchida, John D. Ditmars, and Robert A. Paddock. June 1986, 33 p.

41. A stationary visual census technique for quantitatively assessing community structure of coral reef fishes, by James A. Bohnsack and Scott P. Bannerot. July 1986, 15 p.

42. Effects of temperature on the biology of the northern shrimp, *Pandalus borealis*, in the Gulf of Maine, by Spencer Apollonio, David K. Stevenson, and Earl E. Dunton, Jr. September 1986, 22 p.

43. Environment and resources of seamounts in the North Pacific, by Richard N. Uchida, Sigeiti Hayasi, and George W. Boehlert (editors). September 1986, 105 p.

44. Synopsis of biological data on the porgies, *Calamus arctifrons* and *C. proridens* (Pisces: Sparidae), by George H. Darcy. September 1986, 19 p.

45. Meristic variation in *Sebastes* (Scorpaenidae), with an analysis of character association and bilateral pattern and their significance in species separation, by Lo-chai Chen. September 1986, 17 p.

46. Distribution and relative abundance of pelagic nonsalmonid nekton off Oregon and Washington 1979-84, by Richard D. Brodeur and William G. Pearcy. December 1986, 85 p.

NOAA Technical Report NMFS 51

Status, Biology, and Ecology of Fur Seals

Proceedings of an International Symposium and Workshop Cambridge, England, 23-27 April 1984

John P. Croxall
Roger L. Gentry (*editors*)

June 1987

U.S. DEPARTMENT OF COMMERCE
Malcolm Baldrige, Secretary
National Oceanic and Atmospheric Administration
Anthony J. Calio, Administrator
National Marine Fisheries Service
William E. Evans, Assistant Administrator for Fisheries

Libra.
NOAA, National Marine Fisheries Service
SWFC Honolulu Laboratory F/SWC2
2570 Dole Street
Honolulu, HI 96822-2396

Digitized by the Internet Archive
in 2025

https://archive.org/details/noaa-technical-report-nmfs-ssrf_1987-06_51

CONTENTS

Croxall, John P., and Roger L. Gentry
Introduction to the Proceedings 1

Species Summaries

McCann, T. Seamus, and D. William Doidge
Antarctic fur seal, *Arctocephalus gazella* 5

York, Anne E.
Northern fur seal, *Callorhinus ursinus*, Eastern Pacific Population (Pribilof Islands, Alaska, and San Miguel Island, California) 9

Trillmich, Fritz
Galapagos fur seal, *Arctocephalus galapagoensis* 23

Vaz-Ferreira, Raul, and Alberto Ponce de Leon
South American fur seal, *Arctocephalus australis*, in Uruguay 29

Majluf, Patricia
South American fur seal, *Arctocephalus australis*, in Peru 33

Torres N., Daniel
Juan Fernández fur seal, *Arctocephalus philippii* 37

Fleischer, Luis A.
Guadalupe fur seal, *Arctocephalus townsendi* 43

Mattlin, Robert H.
New Zealand fur seal, *Arctocephalus forsteri*, within the New Zealand region 49

Ling, John K.
New Zealand fur seal, *Arctocephalus forsteri*, in southern Australia 53

Bester, Marthan N.
Subantarctic Fur Seal, *Arctocephalus tropicalis*, at Gough Island (Tristan Da Cunna Group) 57

Kerley, Graham I. H.
Arctocephalus tropicalis on the Prince Edward Islands 61

David, Jeremy H. M.
South African fur seal, *Arctocephalus pusillus pusillus* 65

Shaughnessy, Peter D., and Robert M. Warneke
Australian fur seal, *Arctocephalus pusillus doriferus* 73

Roux, Jean-Paul
Subantarctic fur seal, *Arctocephalus tropicalis*, in French subantarctic territories 79

Contributed Papers

Pierson, Mark O.
Breeding behavior of the Guadalupe fur seal, *Arctocephalus townsendi* 83

Roux, Jean-Paul, and Pierre Jouventin
Behavioral cues to individual recognition in the subantarctic fur seal, *Arctocephalus tropicalis* 95

Stewart, Brent S., Pamela K. Yochem, Robert L. DeLong, and George A. Antonelis, Jr.
Interactions between Guadalupe fur seals and California sea lions at San Nicolas and San Miguel Islands, California 103

Doidge, D. William
Rearing of twin offspring to weaning in Antarctic fur seals, *Arctocephalus gazella* 107

Vladimirov, Valery A.
Age-specific reproductive behavior of northern fur seals on the Commander Islands 113

Kerley, Graham I. H., and Terrence J. Robinson
Skull morphometrics of male Antarctic and subantarctic fur seals, *Arctocephalus gazella* and *A. tropicalis*, and their interspecific hybrids 121

York, Anne E.
On comparing the population dynamics of fur seals 133

Butterworth, Douglas S., Jeremy H. M. David, Lesley H. McQuaid, and Sibusiso S. Xulu
Modeling the population dynamics of the South African fur seal *Arctocephalus pusillus pusillus* 141

Vaz-Ferreira, Raul
Ecology, behavior, and survival of the South American fur seal in Uruguay 165

Guerra C., Carlos, and Daniel Torres N.
Presence of the South American fur seal, *Arctocephalus australis*, in northern Chile 169

Shaughnessy, Peter D., and L. Fletcher
Fur seals, *Arctocephalus* spp., at Macquarie Island 177

Roux, Jean-Paul
Recolonization processes in the subantarctic fur seal, *Arctocephalus tropicalis*, on Amsterdam Island 189

Rapporteurs' Reports

Trillmich, Fritz
Behavior of fur seals 195

McCann, T. Seamus
Male fur seal tenure 197

McCann, T. Seamus
Female fur seal attendance behavior 199

Stirling, Ian, and Jean-Paul Roux
Fur seal vocalizations 201

Kooyman, Gerald L.
Fur seal diving behavior 203

Appendix 1.
List of participants and authors 205

Appendix 2.
Bibliography of recent fur seal literature 207

COVER: Drawing of South African fur seal by Cathy L. Short.

The National Marine Fisheries Service (NMFS) does not approve, recommend or endorse any proprietary product or proprietary material mentioned in this publication. No reference shall be made to NMFS, or to this publication furnished by NMFS, in any advertising or sales promotion which would indicate or imply that NMFS approves, recommends or endorses any proprietary product or proprietary material mentioned herein, or which has as its purpose an intent to cause directly or indirectly the advertised product to be used or purchased because of this NMFS publication.

The 1984 Fur Seal Symposium: An Introduction

JOHN P. CROXALL
British Antarctic Survey
Natural Environment Research Council
High Cross, Madingley Road
Cambridge CB3 OET
United Kingdom

ROGER L. GENTRY
National Marine Mammal Laboratory
National Marine Fisheries Service, NOAA
Seattle, WA 98115
U.S.A.

The 1984 International Symposium and Workshop on the Biology of Fur Seals originated in informal talks in 1981. However, the scope and focus of the symposium remained unclear until an informal workshop was held in San Diego in June 1983. This meeting synthesised data on the foraging and pup attendance activities of six species of fur seals, and attempted to formulate a coherent framework for the adaptations associated with their maternal strategies (Gentry et al. 1986).

During the workshop it was clear that comparative data on many key aspects of fur seal biology and ecology were missing. This absence of data applied not only to less well known species, for some of which considerable unpublished data existed, but also to better known species for which research in some areas had either been neglected or unreported. The value of applying the comparative method to seals, especially comparisons integrating physiology, ecology, and reproductive biology, was amply demonstrated by the results of the 1983 workshop (Gentry and Kooyman 1986). However, we were also aware that many other problems outside the area of maternal strategies could benefit from comparative data, such as recovery of populations from the effects of harvesting. Therefore, to accommodate the range of potential research, we organized this symposium to produce an up-to-date synthesis of relevant information for all species of fur seals.

It was also clear that fur seal research could benefit from increased communication and collaboration among its practitioners. To foster the spread of ideas, we held oral presentations on some topics of current research and techniques and organized workshops on specific topics, in addition to providing opportunities for informal talks among participants. Thanks to generous support from the British Antarctic Survey, the National Marine Fisheries Service of the United States, and the Scientific Committee on Antarctic Research, the International Fur Seal Symposium was held at the British Antarctic Survey, Cambridge, England, 23-27 April 1984. The 36 participants are shown in Figure 1. A list of Symposium participants and authors is presented in Appendix 1 of the Proceedings.

OBJECTIVES

The specific objectives of the meeting were:

1. Review the scope and results of present behavioral, ecological, and physiological research on each species.
2. Review the present status, recent population trends, history of exploitation, and rate of recovery from exploitation for each species.
3. Compare demographic, behavioral, and ecological traits that may be related to recovery for each species.
4. Identify important needs and opportunities for fur seal research, stressing comparisons and collaborative efforts.

The first day of the meeting was devoted to formal presentations designed to introduce participants to recent technical advances in studies of fur seal biology, including experimental and analytical work on fine tooth structure by J. L. Bengtson, diving studies by G. L. Kooyman, and radio isotope and related techniques for bioenergetic studies by D. P. Costa. Also, a variety of presentations introduced aspects of current fur seal research in existing field programs covering most species.

The next four days were organized as a series of round-table workshops with specific sessions devoted to diving, bioenergetics,

Figure 1—Symposium attendees, left to right. Front row: G. I. H. Kerley, L. A. Fleischer, D. Torres. Second row: R. L. Gentry, R. L. DeLong, P. D. Shaughnessy, G. L. Shaughnessy, M. E. Goebel, A. E. York, A. Trites, P. Majluf, T. S. McCann, A. Ponce-de-Leon. Third row: B. Tollu, C. W. Fowler, D. P. Costa, M. N. Bester, G. L. Kooyman, I. Stirling, R. W. Davis, D. W. Doidge, J. L. Bengtson, F. Trillmich, R. Vaz-Ferreira. Back row: P. Jouventin, J.-P. Roux, J. P. Croxall, T. G. Smith, D. M. Lavigne, R. H. Mattlin, J. H. M. David, R. M. Laws, W. N. Bonner, and M. O. Pierson.

diet, growth, onshore attendance, population dynamics, and behavior (including vocalizations). These sessions were especially stimulating and have had a major influence in shaping subsequent fur seal research. The British Antarctic Survey circulated at the workshop a bibliography of recent research on fur seals worldwide, and an updated version of that bibliography is presented in the Proceedings as Appendix 2.

This volume includes reviews of species biology and ecology that were specially commissioned for the workshop, as well as contributed papers dealing with various aspects of recent research on fur seals, and rapporteur's reports on five of the round-table workshops. All papers have been independently reviewed.

An extensive introduction is inappropriate here, since this volume is intended to summarize knowledge of fur seal biology and ecology, and because Bonner (1981), FAO (1982), and Gentry and Kooyman (1986) provide an adequate general background of this group of seals.

Fur seals are one of the two main groups of the Otariidae or eared seals, the other group comprised by five species of sea lions, one species in each of the genera *Eumetopias*, *Neophoca*, *Otaria*, *Phocarctos*, and *Zalophus*. Sea lions and fur seals diverged some two million years ago, and fur seals are believed to have evolved in the northern hemisphere where the earliest fossils are found, although their principal radiation occurred in the southern hemisphere. The monotypic genus *Callorhinus* (northern fur seal) is restricted to the northern hemisphere where one other fur seal species (*Arctocephalus townsendi*) occurs. Six species of fur seals, all in the genus *Arctocephalus*, inhabit the southern hemisphere, and a seventh species is endemic to the Galapagos Islands on the Equator. The approximate breeding distribution of fur seals is shown in Figure 2.

Although fur seals and true seals diverged from carnivore stock probably some 10 million years apart, the fact that they both lead a largely aquatic existence, but need to come on to land to give birth, has resulted in great similarities between the two groups in anatomical and physiological adaptations. Streamlined bodies, with external projections reduced to a minimum, a well developed subcutaneous fat (blubber) layer, and a suite of adaptations for making lengthy and often deep dives in pursuit of prey are particular characteristics. The main differences between them are that fur seals possess external earflaps and use their fore flippers for swimming, the hind flippers functioning only as rudders. In contrast, true seals use their hind flippers for propulsion and thus have their main musculature in the lumbar region and are relatively clumsy and slow moving on land. In contrast, fur seals' main musculature is the thoracic and cervical regions and they are quick and agile. One of the most obvious biological differences between the two groups is in the timing and manner of pup rearing. In true seals the lactation period is brief (1-6 weeks) and the mother usually fasts while she is ashore suckling the pup. In fur seals, lactation lasts 4-12 months (up to 36 months in some tropical species in some years), during which time the mother makes numerous feeding trips to sea, alternating with shorter periods ashore to suckle the pup.

Fur seals are a very homogeneous group, in appearance, social organization (all species are moderately to highly polygymous), and

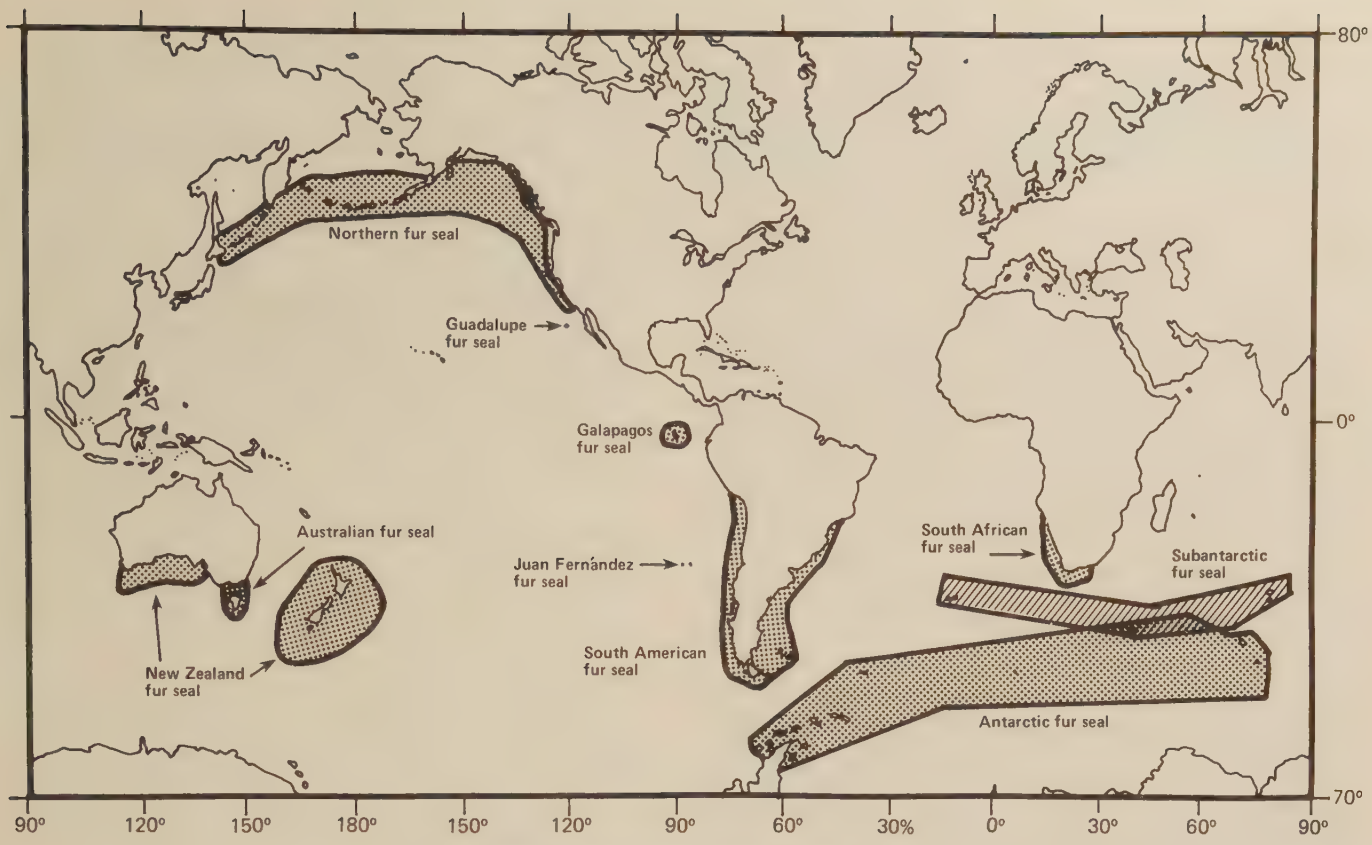


Figure 2—Breeding distribution of fur seals.

basic behavior. However, there is considerable underlying variation in the details of their biology and ecology, some of which has been presented by Gentry et al. (1986; especially tables 15.1-15.3). Complementary data are summarized here in Table 1, and more detailed information is provided in the species summaries in this volume. An important similarity among species of fur seals is that they all have been exploited by man, with several species reduced to the brink of extinction. The extent of past harvesting has focused

Table 1—Selected characteristics of fur seal species.

	Population Size	Status[1]	Adult weight (kg)		Age (yr) at maturity[2]		Pup-rearing period (mo) (max. in parens.)	Food[3]
			Male	Female	Male	Female		
Northern fur seal *Callorhinus ursinus*	1,200,000	—	120-270	30-50	7-10	4	4	1,2
Antarctic fur seal *Arctocephalus gazella*	1,100,000	++	110-200	22-50	7-10	3	4	4,(1,2)
Cape fur seal *A. pusillus*	1,200,000	+	200-360	40-110	?	4	8-12 (18)	1,(2,3)
S. American fur seal *A. australis*	500,00	+	120-150	40-50	7+	4	8-12 (24)	1,(2,3)
Galapagos fur seal *A. galapagoensis*	30,000	+?	60-70	20-35	8-10	4	18-36	1,2
New Zealand fur seal *A. forsteri*	50,000	+?	120-155	40-50	~10	5	10	2,1
Subantarctic fur seal *A. tropicalis*	300,000	++	70-160	25-45	8+	4-5	9-11	1,2,(3)
Guadalupe fur seal *A. townsendi*	1,000	+	~160-170	~40-50	?	?	<12	?
Juan Fernandez fur seal *A. philippi*	6,000	+	(?140)	(?40)	?	?	?	1,2,(3)

[1] – decreasing; + increasing; ++ increasing rapidly.
[2] For females, age of first pupping; for males, age of first harem tenure.
[3] 1 fish; 2 squid; 3 crustaceans, except krill; 4 krill *Euphausia superba*. In order of importance; parentheses denote minor importance.

attention recently on fur seal population dynamics, to monitor the recovery of stocks in some species and to ensure sensible regulation of continuing exploitation in others. Several contributed papers in this volume make important contributions to our knowledge in these fields.

ACKNOWLEDGMENTS

We should like to thank all the Symposium participants for making it such a success, and all authors for their patience and, in many cases, for time spent reviewing papers. We much appreciate additional assistance from J. Harwood, L. Hiby, P. Rothery, T. Smith, J. Thomas, A. G. Wood, and A. E. York. We are greatly indebted to the British Antarctic Survey (BAS), the National Marine Fisheries Service of the United States (NMFS) and the Scientific Committee on Antarctic Research (SCAR) for the financial support that made this meeting possible, and especially to R. M. Laws, Chairman of the SCAR Group of Specialists on Seals, and G. E. Hemmen, Executive Secretary, SCAR, for their advice and encouragement throughout the planning stages. BAS provided considerable assistance in staging this meeting, and we are most grateful to its Director, R. M. Laws, for permission to hold the meeting there.

Invaluable help during the week of the meeting was provided by K. Hartley, R. A. Morgan and C. M. Phillips; W. N. Bonner and T. Seamus McCann also made major organizational contributions to its success. Technical editing was conducted by J. Jones, S. Scott, W. Richards, and N. Peacock. The manuscript was typed by B. Lander and S. Perry.

CITATIONS

BONNER, W. N.
1981. Southern fur seals *Arctocephalus* (Geoffrey Saint-Hilaire and Cuvier, 1826). *In* Ridgway, S. H., and R. J. Harrison, Handbook of marine mammals, Vol. 1., p. 161-208. Academic Press, New York.

FAO ADVISORY COMMITTEE ON MARINE RESOURCES RESEARCH. Working Party on Marine Mammals.
1982. Mammals in the seas, FAO Fish Ser. 5., Vol. 4.

GENTRY, R. L., and G. L. KOOYMAN (editors).
1986. Fur seals: maternal strategies on land and at sea. Princeton Univ. Press.

GENTRY, R. L., D. P. COSTA, J. P. CROXALL, J. H. M. DAVID, R. W. DAVIS, G. L. KOOYMAN, P. MAJLUF, T. S. McCANN, and F. TRILLMICH.
1986. Synthesis and conclusions. *In* Gentry, R.L., and G. L. Kooyman (editors), Fur seals: maternal strategies on land and at sea, p. 220-264. Princeton Univ. Press.

Antarctic Fur Seal, *Arctocephalus gazella*

T. SEAMUS McCANN
British Antarctic Survey
Natural Environment Research Council
High Cross, Madingley Road
Cambridge CB3 OET
United Kingdom

D. WILLIAM DOIDGE
Department of Renewable Resources
MacDonald College of McGill University
21111 Lakeshore Road, Ste-Anne-de-Bellevue
Quebec H9X 1C0
Canada

HISTORY OF HARVESTING

The first known sealing trip to South Georgia was made by an American vessel between 1790 and 1792. The peak of the sealing era was circa 1800-01 when 112,000 skins were taken. Weddell (1825) calculated that by 1822 at least 1.2 million fur seals had been taken from South Georgia and that the population was virtually extinct.

The South Shetland Islands were discovered in 1819, and the first sealing trip was in 1820 by an Argentine vessel. The peak catch was in 1820-21 when approximately 250,000 skins were taken. The smaller stocks at the South Orkney and South Sandwich Islands were also exploited and depleted around this time. No records exist of visits to South Georgia between 1846 and 1870 when sealing was renewed on the partially recovered population there. Occasional sealing trips continued until 1907 when *Daisy* took 170 skins (Bonner 1968). The species has not been commercially exploited since that time.

Exploitation was indiscriminate, with males, lactating females, and juveniles being taken. Black coated pups apparently were not taken.

POPULATION SIZE AND TRENDS

Population estimates are based on pup counts and a knowledge of the age structure of the population. Pup counts were calibrated by marking all pups on selected beaches and by mark-recapture studies (Payne 1978). Payne (1979a) calculated that total population size at the time of weaning was 4.1 times the number of pups born.

The size of the South Georgia population in March 1976 was estimated to total 369,000 animals (Payne 1979a). The population had been increasing at 16.8% annually since the late 1950's (Payne 1977). If this rate of increase has been maintained, which seems likely, then the present (1984) population numbers approximately 1.2 million. Much smaller populations, numbering from a few hundreds to some thousands of animals, occur in the South Shetland, South Orkney, and South Sandwich Islands, Kerguelen, McDonald and Heard Islands, and Bouvetoya and Marion Island (Table 1). All populations appear to be increasing and are believed to have originated from South Georgia (Laws 1973).

INFLUENCES

Space

Historical evidence (Bonner 1968) suggests that, at the time of discovery, large areas of the South Georgia coastline were not occupied by fur seals and that space, therefore, was not a limiting factor. Recolonization of beaches is progressing rapidly at South Georgia, but there are still a number of areas yet to be colonized. Although available breeding space may not be limiting the South Georgia population as a whole (Doidge et al. 1984b), pup production at high-density beaches has stabilized as a result of density-dependent pup mortality (Doidge et al. 1984a) and the emigration of some animals to less dense beaches (Payne 1977; Croxall and Prince 1979; Doidge et al. 1984b). Doidge et al. (1984a) found that preweaning pup mortality was five times greater at high density (17-31% of pup production) than at low density (3-6%). Starvation was the main cause of death and mainly resulted from the failure

Table 1—Survey of Antarctic fur seal populations.

Region	Date of estimate	Population estimate	Pups present	Reference
Scotia Arc				
South Georgia	Mar. 1976	369,000	Y	Payne 1979a
South Orkney	Feb. 1971	2,035	Y	Laws 1973
South Sandwich	1960	400	N	O'Gorman 1961
South Shetland	1957-58	42	Y	O'Gorman 1961
	1981-82	825	?	Cattan et al. 1982
Antarctic Peninsula	?	500	N	Biomass 1984
Subantarctic Islands				
Bouvet	1978-79	4,000	Y	Haftorn et al. 1981
Marion	1981-82	160	Y	Kerley 1983b
Crozet	?	20	N	Jouventin et al. 1982
Kerguelen	Jan. 1980	589	Y	Bester 1981
	1978-81	1,200	Y	Jouventin et al. 1982
Prince Edward	1981-82	200	Y	Kerley 1983b
Heard	Jan.-Feb. 1965	500	Y	Budd and Downes 1969
	?	4,000	Y	Biomass 1984
McDonald	?	300	Y	Biomass 1984
Macquarie	?	<50	?	Biomass 1984

of mother-pup bonding rather than from inadequate food availability for the mother, although in years of krill shortage, pup mortality does increase (Doidge et al. 1984a; McCann unpubl. data). Skull injury caused by bites inflicted by cows and liver rupture resulting from trampling by bulls were the other main causes of death. Preweaning mortality was not different between the sexes. Pups born later in the season suffered disproportionately higher mortality.

Food

If space was not a limiting factor prior to exploitation, then presumably some aspect of food availability was (Doidge et al. 1984b). The principal food of *A. gazella* is krill, *Euphausia superba* (Bonner 1968; Doidge and Croxall 1985). Laws (1977) suggested that the large reduction in stocks of krill-eating whales increased krill availability for other predators. This may have influenced the rate and extent of recovery of the fur seal population, and the population may ultimately exceed its pre-exploited stock size before food becomes limiting. However, local short-term decreases in krill availability affect production in certain years. In 1978-79, there was an apparent shortage of krill at South Georgia which coincided with a twofold increase in preweaning pup mortality (Doidge et al. 1984a) and increased chick mortality in krill-eating seabirds (Croxall and Prince 1979). Similarly, pup mortality was high in 1983-84, continuing through the season, and adult females made longer trips to sea (McCann unpubl. data).

Competitors

Prior to exploitation, krill-eating baleen whales were probably a major competitor for food during the summer. To a certain extent all krill-eating species are competitors, but because of its large population size, similar foraging area, and depth of feeding, the macaroni penguin, *Eudyptes chrysolophus*, is the principal competitor with fur seals for krill in South Georgia waters (Croxall et al. 1985). The winter distribution of female fur seals is unknown, although a migration north of the Antarctic Convergence, equivalent to the southward migration found in *Callorhinus ursinus*, has been postulated (Payne 1979b). Males of all ages remain in the Scotia Sea throughout the year. Fish becomes more important in the diet in winter (North et al. 1983; Brit. Antarct. Survey, Cambridge, unpubl. data), and it is possible that commercial harvesting of fish and potential harvesting of krill could directly affect fur seal population levels (Doidge and Croxall 1985).

Predation

Leopard seals, *Hydrurga leptonyx*, are known to kill fur seal pups and juveniles (McCann pers. observ.). This probably has negligible effects on the total fur seal population since leopard seals are not abundant at South Georgia, and other more typical prey, such as penguins and krill, are freely available. Similarly, killer whales, *Orcinus orca*, are potential predators but are rare around South Georgia. Overall it appears that predation is an insignificant factor in regulating population size.

Survivorship

Payne (1977) used the age structure of breeding females and pup mortality data to estimate age-specific survivorship. First-year mortality was 23.9%, and second-year mortality about 5%. Annual mortality of breeding females was 7.9%. Male survival was assumed to be the same as for females up to age 7, at which age the males begin to gain territorial status and mortality was assumed to increase to 30% (Payne 1977).

REPRODUCTIVE PARAMETERS

In a sample of 195 adult females collected in 1971-72, the age of first pupping was 3 years, when 57% of the females were primiparous (Payne 1977). Twenty-eight percent of females first pupped at age 4 years and 14% at age 5 years. All females had pupped by age 6 years.

Payne (1977) estimated age-specific pregnancy rates to be 0.55 at age 3, 0.75 at age 4, 0.85 at age 5, and 0.90 thereafter. He found no evidence of a decline in pregnancy rates in older animals.

Males are sexually mature at age 3 or 4 but are not recorded to hold territories until age 7 years (Brit. Antarct. Survey, Cambridge, unpubl. data). The oldest territorial bull shot by Payne (1979a) was 11 years old, although animals of up to 14 years have been found dying ashore (Brit. Antarct. Survey, Cambridge, unpubl. data). This suggests that senility may occur in males. The mean age of males 6 years and older that die ashore is 8.8 years (Doidge and Croxall 1985).

REPRODUCTIVE ECOLOGY

At South Georgia, pupping extends from late November to late December, with the median pupping date in the range 4-8 December (Doidge et al. 1984b). At Marion Island in 1981, the mean date of pupping for *A. gazella* was 6 December (SD 8.3 days; Kerley 1983a). Births are highly synchronized, with 90% occurring within 21 days (Payne 1977).

Density of breeding females within groups varies between beaches. On the high-density sites where the seals occupy approximately 50% of the total space, densities reach 1.5 females/m^2 at peak occupancy. At recently colonized sites where an estimated 10% of the available area is occupied, overall female density is about 0.2 females/m^2.

Gregariousness (nearest neighbor distance) also varies with population density. Even where space is freely available, females aggregate and lie within an estimated 30 cm of their nearest neighbor, but not in contact. When space is limited, females permit contact usually in a head-to-tail manner avoiding a head-to-head orientation. However, they never exhibit the thigmotactic behavior seen in sea lions. Group size varies with population density, beach size, and topography. Groups can range in size from two females to several hundred in which groups are not distinguishable.

Males which were observed to copulate did so with an average of 10 cows (McCann 1980). The male:female ratio on crowded beaches at the peak of cow numbers is estimated at 1:10. On less dense beaches some males establish territories in areas not occupied by females and thus fail to copulate.

Adult females haul-out, give birth 2 days later, and then remain ashore for approximately 7 days with the pup during the perinatal attendance period. Lactation lasts 112 days (range 90-126) during which the female makes approximately 16 trips to sea (range 12-21). The mean date of weaning is 1 April (±7 days) (Doidge et al. 1986). At Marion Island, where *A. gazella* is sympatric with the subantarctic fur seal *A. tropicalis*, Kerley (1983a) reported a lactation period of 112 days and a median weaning date of 28 March for Antarctic fur seals. In seasons of average food abundance, foraging trips to sea are approximately 4 days long and alternate with attendance periods ashore of about 2 days (Doidge et al. 1986). In years of krill shortage, time spent ashore decreases together with an increase in feeding trip duration.

GROWTH

Payne (1979a) gives full details of weight-at-age for a large sample of males and females. Breeding females range in weight from 22 to 50 kg and territorial bulls from 110 to 230 kg (Brit. Antarct. Survey, Cambridge, unpubl.). Doidge and Croxall (1985) calculated average weights for adults, juveniles, and weaners as 125, 38, and 17 kg for males and as 32, 16, and 14 kg for females, respectively.

Payne (1979a) found birth weights of male pups to be 5.9 ± 0.5 kg (n = 9, range 4.9-6.6 kg) and female pups 5.4 ± 0.3 kg (n = 12, range 4.8-5.9). Using two seasons of pup weight data from Payne (1979a) and an additional four seasons of pup weighings, Doidge et al. (1984b) found that male pup growth averaged 90 g/day and female pup growth 76 g/day. Although growth rates varied between seasons, no systematic decrease in growth rate or birth weight was found during a period (1972-81) when the South Georgia population size had probably quadrupled (Doidge et al. 1984b).

FOOD

Diet has been summarized in Doidge and Croxall (1985). Females feed primarily on mature krill ranging in length from 35 to 65 mm. Fish are also taken in small numbers, but the frequency is unknown. Penguins are eaten but make up only about 1% of the diet during the summer. North et al. (1983) examined the fish component of the diet of juvenile males in which the pelagic icefish, *Chamsocephalus gunnari*, predominated by weight (76%) and number (55%). Other species consumed included the lantern fish, *Gymnoscopelus nicholsi*, and the nototheniids *Notothenia rossii*, *N. gibberifrons*, *N. larseni*, and *Pseudochaenichthys georgianus*. These fish are epipelagic, associated with krill swarms, and presumably taken opportunistically by the seals. North et al. (1983) and Doidge and Croxall (1985) stress the inadequate knowledge of fur seal diet. Bonner and Hunter (1982) noted that subadult males have been observed to kill but only infrequently eat macaroni penguins.

CURRENT RESEARCH ON *A. GAZELLA* AT SOUTH GEORGIA

Data associated with long-term monitoring and research studies of trophic relationships in the southern ocean will continue to be collected at Bird Island, South Georgia. These include further study of the diet and energy requirements of all year classes; maternal feeding attendance behavior, maternal condition, and the relationship of these factors to pup growth and survival.

A 5-year study of factors affecting male breeding success was started in the 1984-85 field season. A reservoir of known-age animals will continue to be built-up on selected beaches by tagging pups. However, because of the problems of emigration from natal beaches, tag-recapture methods are not thought to be useful in calculating population size or age-specific survivorship until more is known about juvenile movement patterns. The South Georgia population should be censused within the next 5-10 years using aerial photography.

Detailed analysis of male and female time-activity budget data nears completion at the British Antarctic Survey. Studies of reproductive energetics and fine tooth structure are being carried out with collaborators from the United States.

CITATIONS

BESTER, M. N.
1981. Fur seals *Arctocephalus gazella* and leopard seals *Hydrurga leptonyx* at the Courbet Peninsula, Kerguelen. S. Afr. J. Antarct. Res. 10/11:35-38.

BIOMASS.
1984. Report of the meeting of the SCAR group of specialists on seals, Pretoria, 7-8 September, 1983. Sci. Comm. Antarct. Res., Biomass Rep. Ser. 35.

BONNER, W. N.
1968. The fur seal of South Georgia. Br. Antarct. Surv. Sci. Rep. 56:1-81.

BONNER, W. N., and S. HUNTER.
1982. Predatory interactions between Antarctic fur seals, macaroni penguins and giant petrels. Br. Antarct. Surv. Bull. 56:75-79.

BUDD, G. M., and M. C. DOWNES.
1969. Population increase and breeding in the Kerguelen fur seal *Arctocephalus tropicalis gazella*, at Heard Island. Mammalia 33:58-67.

CATTAN, P. E., J. YANEZ, D. TORRES, M. GAJARDO, and J. C. CARDENAS.
1982. Censo, marcaje y estructura poblacional del lobo fino antarctico *Arctocephalus gazella* (Peters, 1875) en las islas Shetland del Sur, Chile. Inst. Antárt. Chileno Serie Cientifica 29:31-38.

CROXALL, J. P., and P. A. PRINCE.
1979. Antarctic sea bird and seal monitoring studies. Polar Rec. 19:573-595.

CROXALL, J. P., P. A. PRINCE, and C. RICKETTS.
1985. Relationships between prey life cycles and the extent, nature and timing of seal and seabird predation in the Scotia Sea. *In* Siegfried, W. R., P. Condy, and R. M. Laws (eds.), Nutrient cycling and food webs in the Antarctic: The Proceedings of the Fourth SCAR Symposium on Antarctic Biology, p. 516-533. Springer Verlag, Berlin.

DOIDGE, D. W., and J. P. CROXALL.
1985. Diet and energy budget of the Antarctic fur seal *Arctocephalus gazella*. *In* Siegfried, W. R., P. Condy, and R. M. Laws (eds.), Nutrient cycling and food webs in the Antarctic: The Proceedings of the Fourth SCAR Symposium on Antarctic Biology, p. 543-550. Springer Verlag, Berlin.

DOIDGE, D. W., J. P. CROXALL, and J. R. BAKER.
1984a. Density dependent pup mortality in the Antarctic fur seal *Arctocephalus gazella* at South Georgia. J. Zool. (Lond.) 202:449-460.

DOIDGE, D. W., J. P. CROXALL, and C. RICKETTS.
1984b. Growth rates of Antarctic fur seal pups at South Georgia. J. Zool. (Lond.) 203:87-93.

DOIDGE, D. W., T. S. McCANN, and J. P. CROXALL.
1986. Attendance behavior of Antarctic fur seal *Arctocephalus gazella*. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur Seals: Maternal Strategies on Land and at Sea, p. 102-114. Princeton Univ. Press. Princeton, NJ.
HAFTORN, S., L. SOMME, and J. S. GRAY.
1981. A census of penguins and seals on Bouvetoya. Nor. Polarinst. Skr. 175:29-35.
JOUVENTIN, P., J. C. STAHL, and H. WEIMERSKIRCH.
1982. La recolonisation des iles Crozet par les otaries (Fur seal recolonization of the Crozet Islands) *Arctocephalus tropicalis* and *A. gazella*. Mammalia 46:505-514.
KERLEY, G. I. H.
1983a. Comparison of seasonal haulout patterns of fur seals *Arctocephalus tropicalis* and *A. gazella* on subantarctic Marion Island. S. Afr. J. Wildl. Res. 13:71-77.
1983b. Relative population sizes, trends and hybridization of fur seals *Arctocephalus tropicalis* and *A. gazella* at the Prince Edward Islands, Southern Ocean. S. Afr. J. Zool. 18:388-392.
LAWS, R. M.
1973. Population increase of fur seals at South Georgia. Polar Rec. 16:856-858.
1977. Seals and whales of the Southern Ocean. Philos. Trans. R. Soc. Lond. B 279:81-96.
McCANN, T. S.
1980. Territoriality and breeding behavior of adult male Antarctic fur seals *Arctocephalus gazella*. J. Zool. (Lond.) 192:295-310.
NORTH, A. W., J. P. CROXALL, and D. W. DOIDGE.
1983. Fish prey of the Antarctic fur seal *Arctocephalus gazella* at South Georgia. Br. Antarct. Surv. Bull. 61:27-37.
O'GORMAN, F. A.
1961. Fur seals breeding in Falkland Islands Dependencies. Nature 192:914-916.
PAYNE, M. R.
1977. Growth of a fur seal population. Philos. Trans. R. Soc. Lond. B 279:67-79.
1978. Population size and age determination in the Antarctic fur seal *Arctocephalus gazella*. Mammal Rev. (8):67-73.
1979a. Growth in the Antarctic fur seal *Arctocephalus gazella*. J. Zool. (Lond.) 187:1-20.
1979b. Fur seals *Arctocephalus tropicalis* and *A. gazella* crossing the Antarctic Convergence at South Georgia. Mammalia 43:93-98.
WEDDELL, J.
1825. A voyage towards the South Pole, performed in the years 1822-24. Longman, Hurst, Rees, Orme, Brown and Green, London, 324 p.

Northern Fur Seal, *Callorhinus ursinus*, Eastern Pacific Population (Pribilof Islands, Alaska, and San Miguel Island, California)

ANNE E. YORK
National Marine Mammal Laboratory
National Marine Fisheries Service, NOAA
7600 Sand Point Way N.E., Bldg. 4
Seattle, WA 98115

INTRODUCTION

The breeding islands and general oceanic distribution of the northern fur seal, *Callorhinus ursinus*, are shown in Figure 1. A new rookery was discovered on Bogoslof Island, Alaska, in 1980 (Lloyd et al. 1981); at least 11 pups were born there in 1983 (Loughlin 1985).

The species is pelagic during most of the year. The pelagic distribution is generally segregated: females from the Pribilof Islands herd are found in the southern part of the range and males in the northern part of the range, with some overlap in the Gulf of Alaska. The pelagic distribution of seals of San Miguel Island origin has not been extensively studied.

Adult males arrive on the breeding areas in mid-May and early June and establish territories. Males maintain territories until early August. Pregnant females arrive during mid-June to early August; they give birth within one-two days to a single pup and breed within the following week. The postpartum females then begin a series of feeding-nursing cycles of several days. Pups are weaned in October-November and begin their pelagic life; they may or may not return to the breeding island after their first year. Females and males return to sea until the next breeding season. Peterson (1968) summarized population sizes of various components of the herd on the rookery during the breeding season (Fig. 2).

HISTORY OF HARVESTING

The history of fur seal exploitation on the Pribilof Islands from the time of their discovery in 1786 to 1979 is summarized in Figure 3 (Lander 1980). General accounts of management and related research during this period are found in Scheffer et al. (1984) and Roppel (1984).

Lander (1980) summarizes the history of northern fur seal exploitation:

> Early exploitation was unregulated and excessive until 1799 when the Russian-American Company was put in control of the fur seal harvest. Despite various temporary bans on commercial killing, the fur seal harvest declined, and in 1834 the Russian-American Company severely restricted the land harvest of males and banned the killing of females altogether. At this time the fur seal herd was at its lowest level during the Russian tenure on the Pribilof Islands. The harvest restrictions and ban on taking females enabled the herd to recover and by 1867, when the United States purchased Alaska, several thousand males were taken each year. General accounts of management and related research during this period are found in Scheffer et al. (1984) and Roppel (1984).
>
> An unregulated harvest by independent parties in the first 2 years of American occupation took nearly 250,000 fur seals. The U.S. government then set aside the Pribilof Islands as a special reservation for the protection of fur seals and in 1870 began a series of leasing arrangements with private companies for the harvest rights which lasted until 1909. During this period the harvest on land was closely regulated through the leasing agreements but an uncontrolled pelagic harvest of fur seals (mostly females) by commercial sealers began shortly after the U.S. purchase of Alaska. From about 1868 until 1911 over 600,000 fur seal skins were taken pelagically and many more

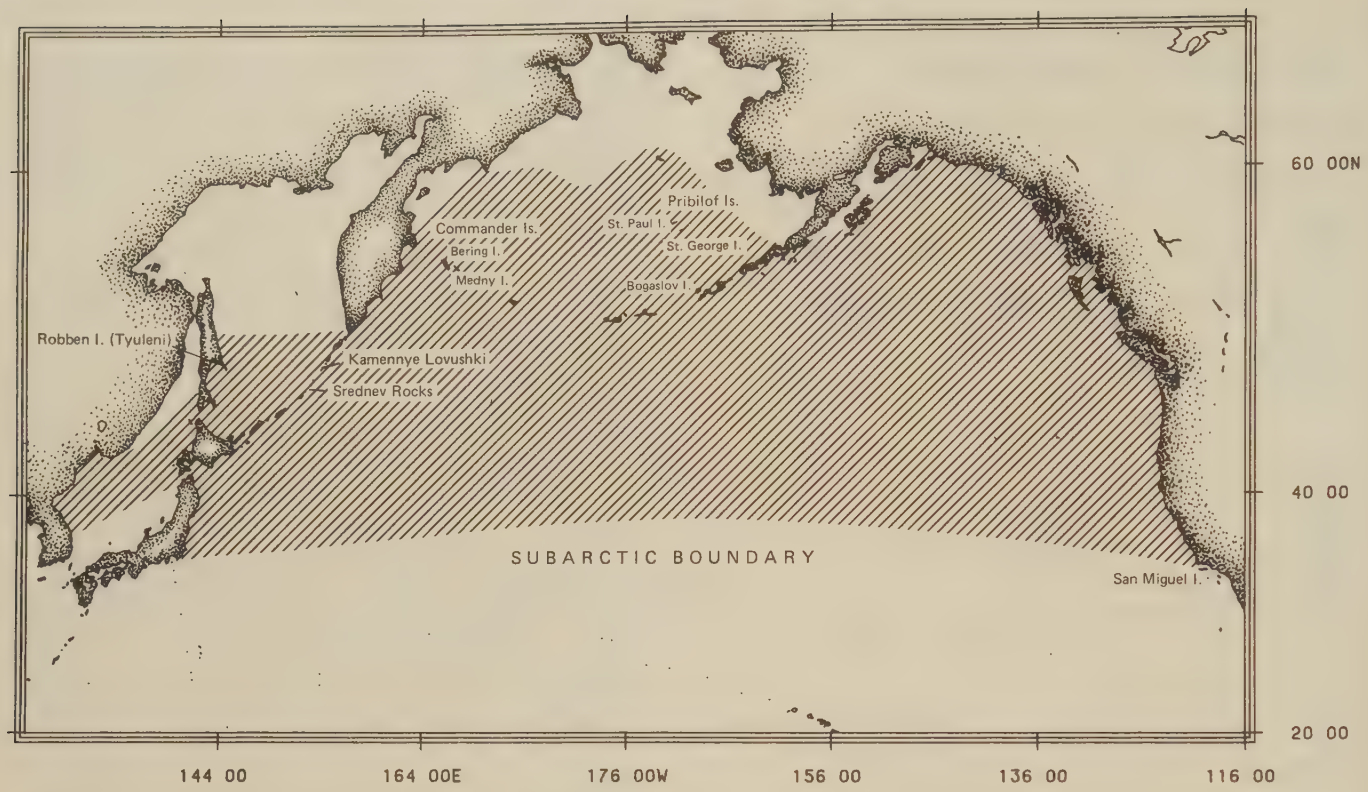


Figure 1—General oceanic distribution and breeding islands of the northern fur seal (after Lander and Kajimura 1982).

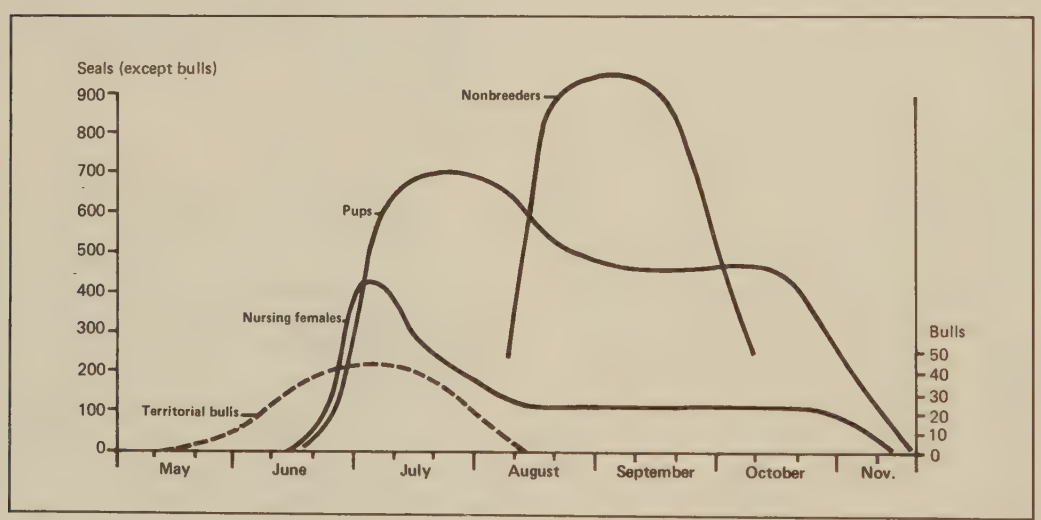


Figure 2—Counts of northern fur seal territorial bulls, nursing females, pups, and nonbreeders on Kitovi Rookery, St. Paul Island, Alaska (from Peterson 1968).

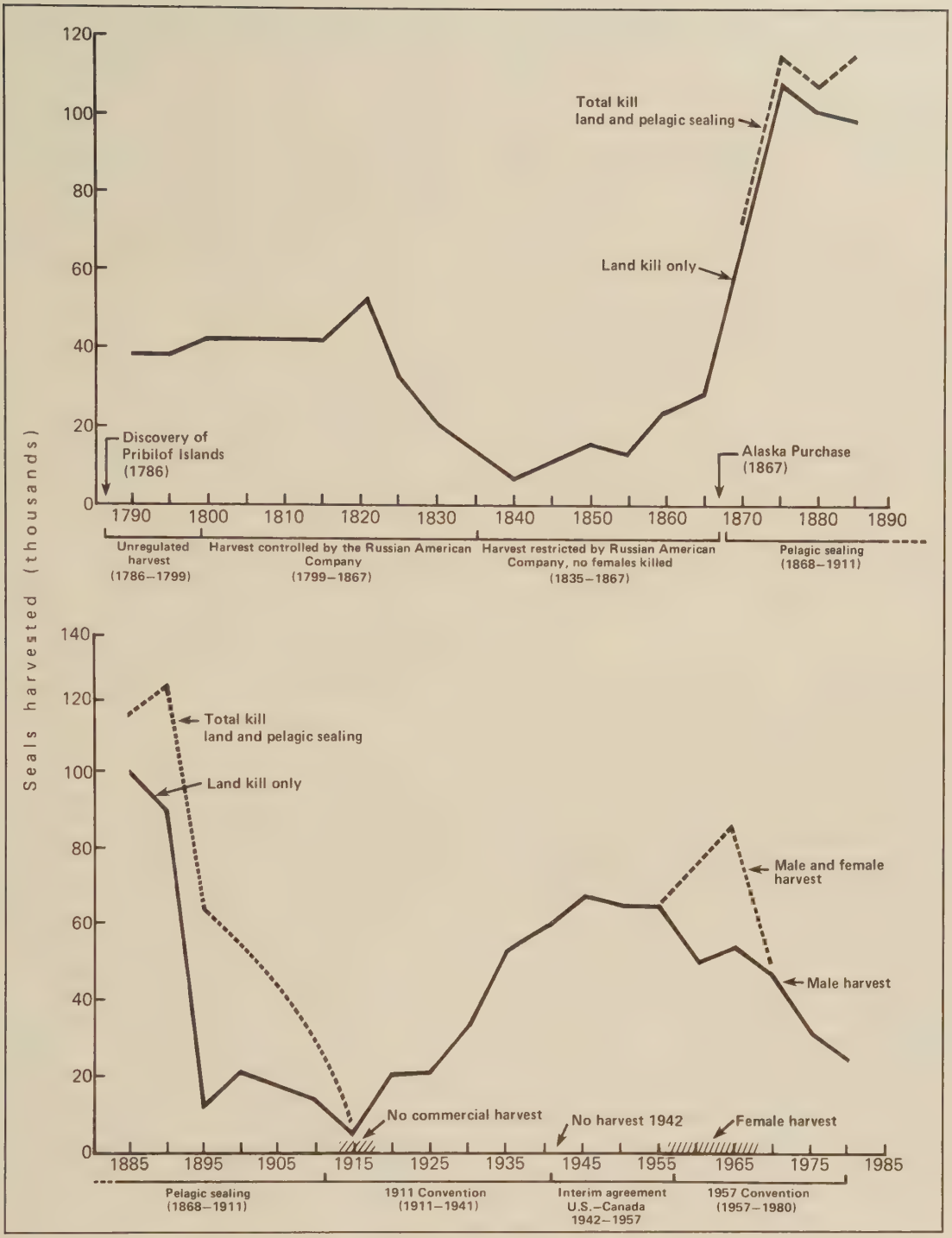


Figure 3—History of northern fur seal exploitation, 1786-1979, Pribilof Islands, Alaska. Data are 5-year averages (from Lander 1980).

animals were undoubtedly killed and not recovered. Most of the pelagic harvest consisted of females of reproductive age and the effect on the Pribilof Island fur seal herd was devastating. By 1909 the herd had dwindled to about 300,000 animals.

In 1911 the North Pacific Fur Seal Convention was negotiated between the United States, Great Britain (for Canada), Japan, and Russia. Commercial pelagic sealing was forbidden by this Convention. In addition, the U.S. Congress prohibited commercial sealing on land from 1912 until 1917. The 1911 Convention remained in effect until 1941 when Japan abrogated the treaty. During this time the herd grew rapidly as did the harvests which concentrated on 3-year-old males. An interim agreement between the United States and Canada protected the herd until 1957 when a new North Pacific Fur Seal Convention was negotiated by the United States, Canada, Japan, and the Soviet Union.

The herd sustained an annual harvest of about 50,000-60,000 subadult male fur seals from 1940 through the late 1950's. In 1956, a commercial harvest of females was begun. It was thought that

a reduction of the herd would increase the maximum sustained yield by increasing pregnancy rates and survival of females (York and Hartley 1981). The commercial harvest of females ended in 1968; approximately 300,000 females were killed on both St. Paul and St. George Islands during this operation. York and Hartley (1981) have modeled the effect of the female harvest on the production of pups and the subsequent decline in the harvest of subadult males on St. Paul Island.

In 1973, St. George Island was declared a research sanctuary and the harvest (except for a small subsistence take of 300-500 animals) was suspended. During 1974-84, the harvest of subadult males on St. Paul declined slightly (about 2% per year). However, the age composition of the harvest changed—numbers of 3-year-old animals in the harvest have remained stable, numbers of 2-year-olds have increased at 10% per year, numbers of 4-year-olds have decreased at about 7% per year, and numbers of 5-year-olds have decreased at about 12% per year. The average age of the harvested population has declined from 3.6 years in 1974 to 3.2 years in 1983. There has been no commercial harvest on St. Paul Island since 1984.

POPULATION SIZE AND TRENDS

Pups

Figure 4 presents the available estimates of numbers of pups born on St. Paul and St. George Islands for 1912-85. York and Kozloff (1987) discuss the methods of determining the numbers of pups born during that period.

During 1912-24, live pups were counted directly. Dead pup counts were then made, and the total number of pups born was estimated as the sum of the live and dead pup counts. For 1925-40, projection estimates were made each year, based on an average growth rate of 8% determined from the data for 1912-24. During the early 1940s, it became obvious that the projection method was not correct, and research on the size of the herd was planned. These plans were interrupted by World War II. York (in Kozloff 1982) was able to estimate the size of the 1940 year class on St. Paul Island from counts of dead and live pups on a sample rookery and counts of harem bulls on the whole island. Estimates of the size of the 1950-60 year classes are from Chapman (1964). These estimates are based on counts of harem and idle males and on a life table for males which assumes constant natural mortality and escapement from the harvest. Estimates of the numbers of pups born after 1961 are mark-recapture estimates. A number of pups are marked throughout the rookery. (For 1961 the marks were tags; from 1962 to present, the mark was made by shearing a small patch of fur from the top of the pups' heads; this exposes the silver colored underfur and makes a visible mark.) On at least two occasions following the shearing, workers traverse the rookery and count the number of marks among subgroups of 25 pups. The estimate of the number of pups alive at the time of the survey is the ordinary Petersen estimate based on the fraction of marked pups among all pups counted and the known number of sheared pups. Counts of dead pups are made and added to the estimate of live pups to produce an estimate of the total number of pups born.

Censuses of pup numbers on St. George Island have not been made as frequently as on St. Paul. For the 1950's, pup numbers on St. George Island were approximated at 20% of the total production on both islands or 25% of the St. Paul production. In 1985, pup production on St. George Island was about 17% of the production on St. Paul Island. During 1975-81 the number of pups born on St. Paul Island declined at approximately 7.8% per year; since 1981 there has been no significant decline in the number born (Fig. 4). The situation is less clear on St. George Island because censuses are conducted there less often. However, current pup production on St. George Island is about 65% of production during 1977-78. The number of pups born on San Miguel Island increased by approximately 34% per year during the period 1967-69 (DeLong 1982). The number of pups born on San Miguel Island was approximately 1,500 in 1981.

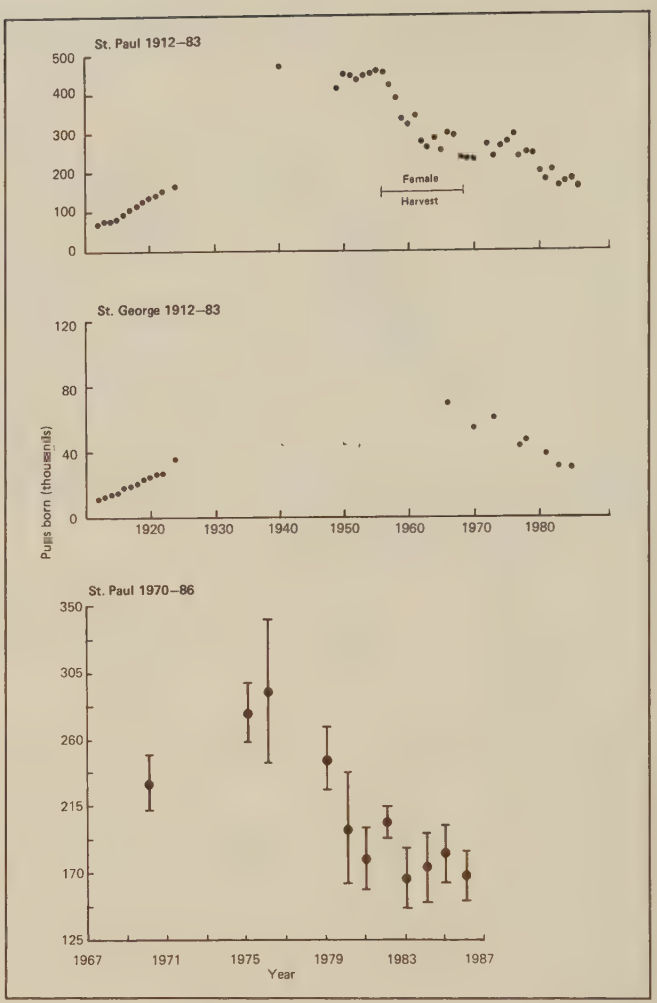


Figure 4—Estimates of numbers of northern fur seal pups born on St. Paul Island, 1912-83 and 1970-86, and on St. George Island, 1912-83.

Adult females

No direct estimates of adult females are made on the Pribilof Islands, except in small study areas for behavioral studies. Instead, the number of adult females is estimated by dividing the number of pups born by the weighted average pregnancy rate of adult females; this is approximately 60% of females 3 years and older or 68% of females 4 years and older. Thus it is difficult to determine if the population of adult females is actually decreasing at the same rate as the number of pups born because the manner of estimating their numbers presumes that the average pregnancy rate has remained constant since the end of the pelagic sampling program 1958-74, the period during which data were collected for estimating these pregnancy rates.

Direct counts of females are made on San Miguel Island. Due to the attendance patterns of females and lack of knowledge of the average pregnancy rate of all females on San Miguel Island (this is a rapidly growing herd with immigration from other populations contributing to the increase), the actual number of females in the San Miguel herd is not known. However, the maximum count of females increased at the rate of about 22% per year during 1967-79 and totaled about 1,100 animals in 1981. (The total number of females in the San Miguel Island population is much larger than 1,100 females, but exact numbers are not known.)

Adult males

Counts of harem males (adult males maintaining territories with females present) and counts of idle males (adult males maintaining territories with no females) have been made most years since 1911 on the Pribilof Islands; these counts represent the longest time-series of counts for any component of the Pribilof Island population. The counts of harem males are more reliable than those of the idle bulls since the latter group is more difficult to define and definitions have not been verifiably consistent throughout the years.

Figure 5 shows the counts of adult males on St. Paul and St. George Islands during 1911-83. Total numbers of adult males on St. Paul Island have decreased by about 2% per year since 1977. On St. George Island, the total number of adult males increased rapidly following termination of the harvest in 1972 until 1979. However, their numbers have declined somewhat since then.

Survivorship

At least three life tables for female fur seals have appeared in the literature (Kenyon et al. 1954; York and Hartley 1981; Lander 1981). The most recent life table for males appears in Lander (1981). Lander (1979a) produced estimates of juvenile survival for the 1950-70 cohorts of males, and York (in Kozloff 1982) extended the results to the 1970-76 cohorts. Lander's life tables appear in Table 1, and estimates of juvenile survival (birth to age 2 years) for the 1950-76 cohorts for which data were available are in Table 2.

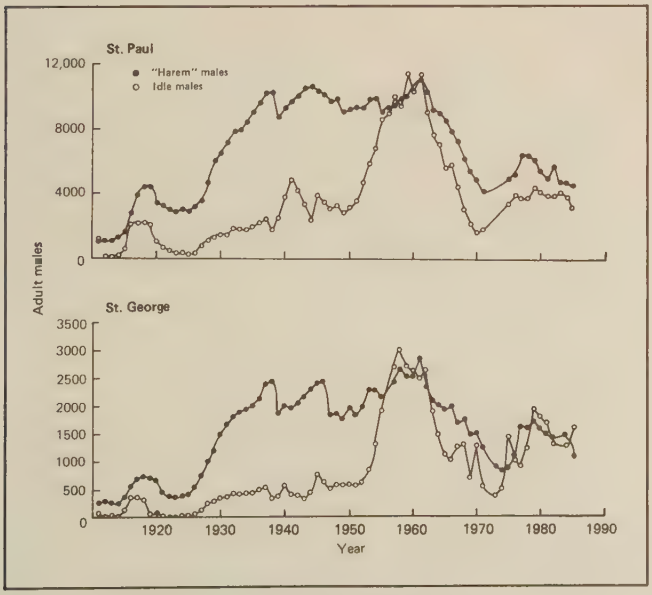


Figure 5—Harem and idle bull counts of northern fur seals on St. George Island and St. Paul Island, Alaska, 1911-82.

Table 1—Summary of age-specific and cumulative survival rates for northern fur seals (from Lander 1981).

	Males				Females	
	St. Paul Island		St. George Island and Sea Lion Rock			
Age	By age	From age 0	By age	From age 0	By age	From age 0
0		1.000		1.000		1.000
1	0.500	0.500	0.400	0.400	0.500	0.500
2	0.760	0.380	0.750	0.300	0.800	0.400
3	0.778	0.296	0.800	0.240	0.840	0.336
4	0.478	0.141	0.800	0.192	0.920	0.309
5	0.342	0.048	0.750	0.144	0.940	0.290
6	0.682	0.033	0.700	0.101	0.940	0.273
7	0.800	0.026	0.650	0.066	0.945	0.258
8	0.800	0.021	0.600	0.040	0.950	0.245
9	0.800	0.017	0.550	0.022	0.950	0.233
10	0.760	0.013	0.500	0.011	0.938	0.219
11	0.730	0.009	0.450	0.005	0.924	0.202
12	0.700	0.006	0.400	0.002	0.906	0.183
13	0.650	0.004	0.320	0.001	0.884	0.162
14	0.590	0.002	0.220	<0.001	0.858	0.139
15	0.540	0.001	0.100		0.876	0.122
16	0.430	<0.001	0.010		0.789	0.096
17			<0.010		0.743	0.071
18					0.692	0.044
19					0.630	0.031
20					0.564	0.017
21					0.490	0.008
22					0.411	0.003
23					0.330	0.001
24+					<0.330	<0.001

Table 2—Estimates of survival of juvenile male and female northern fur seals, based on Lander (1975). Estimates for 1950-70 cohorts appeared in Lander (1979a), and estimates for the 1972-76 cohorts are from York (1982).

	Male			Female
Cohort	Survival on land (0-4 mo)	Survival at sea (4 mo-2 yr)	Survival (0-2 yr)	Survival (0-2 yr) (1.1 × male surv.)
50	0.88	0.41	0.36	0.40
51	0.84	0.42	0.35	0.39
52	0.91	0.46	0.42	0.46
53	0.82	0.38	0.31	0.34
54	0.79	0.30	0.24	0.26
55	0.84	0.33	0.28	0.30
56	0.78	0.18	0.14	0.15
57	0.85	0.37	0.31	0.35
58	0.92	0.49	0.45	0.50
59	0.88	0.43	0.38	0.42
60	0.81	0.34	0.28	0.30
61	0.83	0.39	0.32	0.36
62	0.84	0.43	0.36	0.40
63	0.88	0.47	0.41	0.45
64	0.92	0.47	0.43	0.48
65	0.85	0.41	0.35	0.38
66	0.92	0.36	0.33	0.36
67	0.95	0.42	0.40	0.44
68	0.89	0.42	0.37	0.41
69	0.94	0.38	0.36	0.39
70	0.91	0.46	0.42	0.46
72	0.92	0.33	0.30	0.33
73	0.91	0.36	0.33	0.36
74	0.95	0.33	0.31	0.34
75	0.93	0.31	0.29	0.32
76	0.92	0.31	0.29	0.31

The published life tables are quite similar, and all of them, when coupled with estimates of female juvenile survival (birth to age 2 years) and age-specific pregnancy rates, can satisfactorily predict the numbers of pups born for the years 1950-83. However, no direct estimates of female juvenile survival are available, and to successfully model numbers of pups born, most researchers have made assumptions about the relationship of male and female juvenile survival. Chapman (1964) inferred that the survival of juvenile female fur seals was about 10% higher than males. I have determined that the best estimate of the ratio of female-to-male juvenile survival rates is dependent on the life table used. For the life tables in Kenyon et al. (1954) and York and Hartley (1981), the 10% figure is reasonable; however, if the Lander (1981) life table is used, a 5% figure is better based on the reliability of predictions of the numbers of pups born.

Influences

Clearly the greatest influence on the population of fur seals during the past 30 years has been the herd reduction accomplished through a harvest of females. It is not understood how other factors influence the course of the population over time because their effects are not nearly so drastic. Mortality during the first 4 months of life appears to be density-dependent (York in Kozloff 1982). Common causes of death among pups are starvation, trauma, and diseases (hookworm and leptospirosis). Space is not a limiting factor on the Pribilof Islands or on San Miguel Island at present. Sharks, killer whales (*Orcinus orca*), and Steller's sea lions (*Eumetopias jubatus*) are known to prey on fur seals (Scheffer et al. 1984); Gentry and Johnson (1981) estimated that sea lions consumed 3.4-6.8% of neonates on St. George Island during the summers of 1974 and 1975. A small percentage of males in the commercial harvest (about 0.45%) carry netting or other debris when they appear in the harvest; Fowler (1982) estimated that mortality due to entanglement in debris could be as much as 5% per year. Incidental catch in commercial fisheries is insignificant (Loughlin et al. 1983).

REPRODUCTIVE PARAMETERS

Age at first pupping

York (1983) developed three methods of estimating age at first pupping for the 1952-66 cohorts based on data collected at sea by scientists from the United States and Canada during 1958-74. Age at first pupping did not apparently behave in a stereotypical density-dependent fashion following reduction of the herd. In fact, age at first pupping appears to have increased sharply, then decreased slowly with the decrease of the population; it never returned to the low level of those cohorts born before the herd reduction. Figure 6a shows the percentage of females pregnant at least once and the percentage primiparous and pregnant when sampled. Figure 6b shows the relationship between estimated age at first reproduction and juvenile survival (birth to age 2 years). Age at first reproduction and juvenile survival are negatively correlated, but the level of age at first reproduction is 0.6 years higher for the 1956-66 cohorts than for the 1952-55 cohorts. York (1983) postulates that this difference could have been caused by (1) the manner in which commercial harvest of females was conducted (a higher percentage of earlier maturing females harvested would leave more later maturing animals to be sampled) or (2) possible positive bias in the estimates of numbers of pups born during the 1950s.

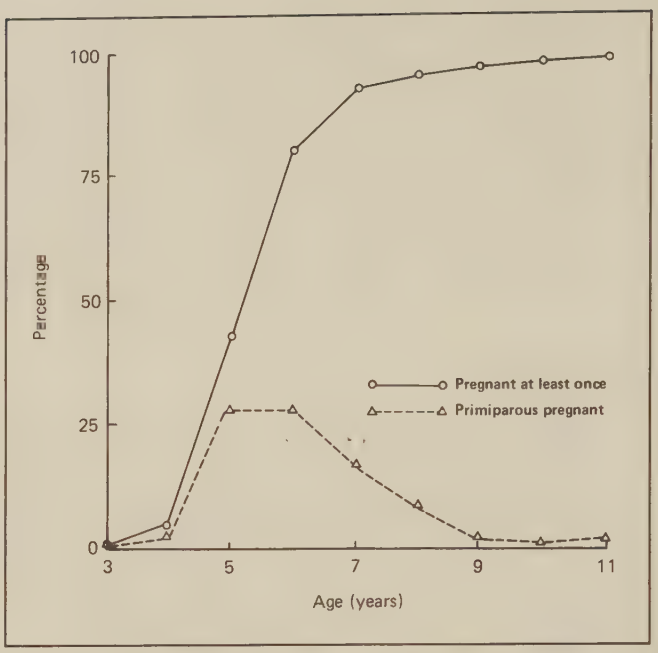


Figure 6a—Percentage of female northern fur seals pregnant at least once (parous) and percentage primiparous and pregnant as a function of age for the 1954-64 year classes based on data from the combined United States-Canadian pelagic collections 1958-74 (from York 1983).

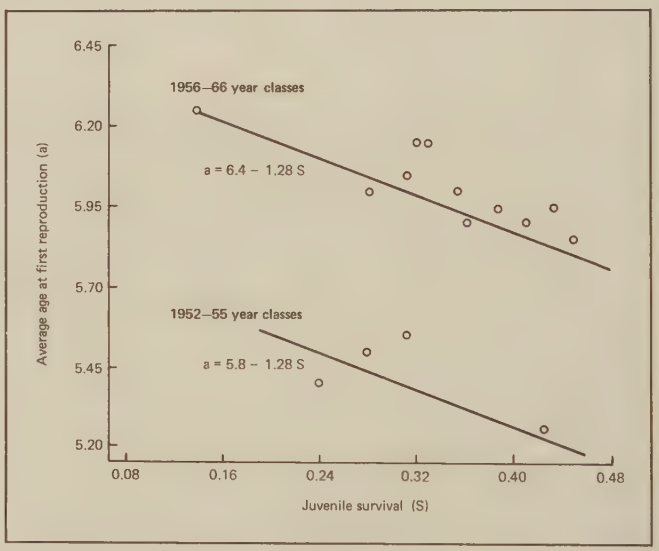


Figure 6b—Age at first reproduction of female northern fur seals as a function of Lander's (1979a) juvenile survival estimates for the 1952-66 year classes. Age is regressed on survival with separate intercepts for the 1952-55 and 1956-64 year classes (from York 1983).

Age-specific fecundity

The age-specific pregnancy rates based on data from the pelagic sampling program (1958-74) appear in York and Hartley (1981). Since the sex ratio of fetuses did not vary significantly from 1:1, the age-specific fecundity rates (number of females born to each female) are assumed to be 0.5 of the age-specific pregnancy rates (Table 3). York (1980) showed that pregnancy rates among females 7 years and older did not change significantly during the period of the pelagic investigations, although there was some year-to-year variation. However, among those age groups which were not fully

Table 3—Pregnancy and fecundity rates for female northern fur seals. Pregnancy rates from York and Hartley (1981).

Age	Pregnancy rate	Fecundity
2	0.00	0.00
3	0.00	0.00
4	0.05	0.03
5	0.35	0.18
6	0.71	0.35
7	0.80	0.40
8	0.87	0.43
9	0.88	0.44
10	0.88	0.44
11	0.89	0.45
12	0.86	0.43
13	0.86	0.43
14	0.83	0.42
15	0.82	0.41
16	0.79	0.39
17	0.70	0.24
18	0.64	0.32
19	0.54	0.27
20	0.47	0.23
21	0.50	0.25
22	0.28	0.14
23	0.11	0.05
24	0.00	0.00
25	0.00	0.00

Table 4—Age composition of breeding northern fur seal males killed as part of study and mature males found dead on land in 1965 (Johnson 1968).

Age	Number of seals
7	7
8	31
9	48
10	101
11	87
12	35
13	54
14	23
15	12
16	6
17	1
18	0
Total	405

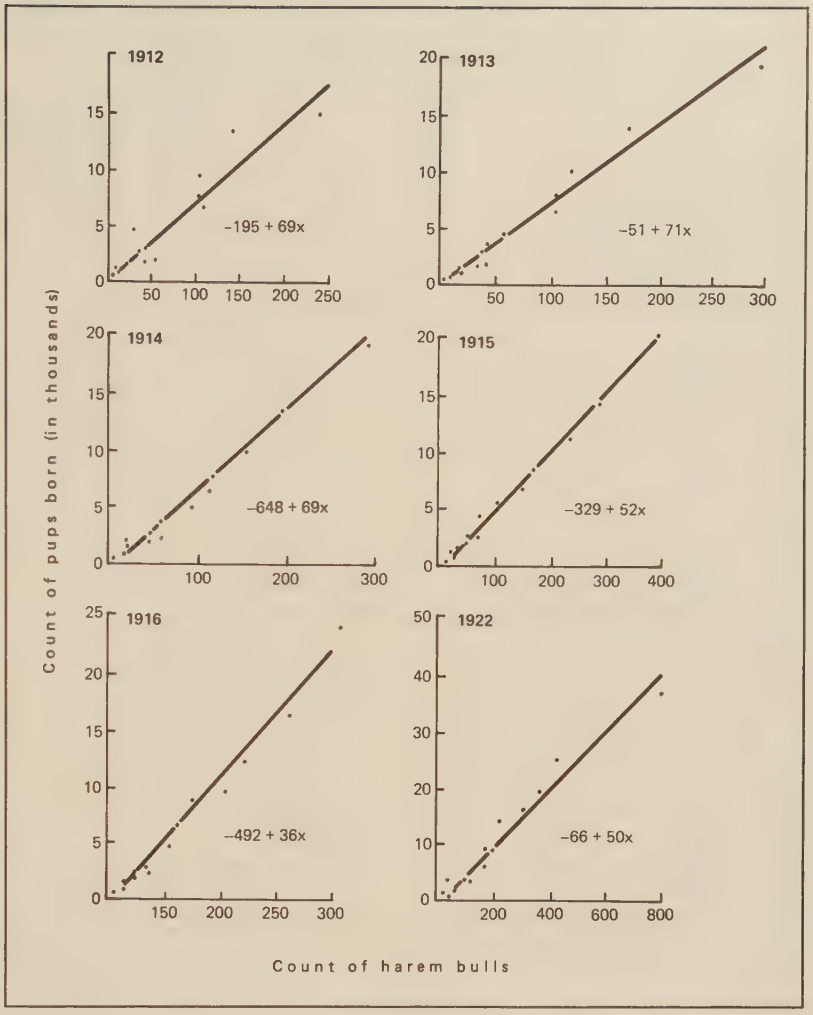


Figure 7a—Relationship of counts of northern fur seal pups born to counts of harem bulls for the various rookeries of St. Paul Island, Alaska, 1912-22 (from York and Kozloff 1987).

recruited to the breeding population, the pregnancy rates did change over time. This was the basis for conducting the analysis of the change in age at first reproduction, discussed above.

Age of attainment of territorial status in males

No information is available concerning the attainment of territorial status. However, information is available on the age composition of males holding territories with females (harem males). Table 4 contains the age composition of 405 breeding males killed or found dead on land in 1965. The average age is 10.93 years (SD = 1.97 years).

REPRODUCTIVE ECOLOGY

Timing and duration of the pupping season

On the Pribilof Islands, pups are born from 15 June to 1 August. The median date of births on St. Paul Island is 7-8 July (Peterson 1968). The pupping season on San Miguel Island is usually from late May to late July; the length of the pupping season is 4-7 weeks, and the median birth date is about 2 weeks earlier than on the Pribilof Islands (24 June with a range of 21-29 June over the 10-year period 1969-78) (DeLong 1982).

Density of females

Gentry (in Kozloff 1980) reported a peak density of 1.75 (SD = 0.34) females/m^2 at study areas on St. George Island during 1974-79. Within a group, density is greatest in the first week that females are on shore, and it declines during the season.

Degree of polygyny

York and Kozloff (1987) have examined the historical data regarding the sex ratio of breeding adults. The ratio of pups to breeding males is remarkably constant among rookeries for a given season (Fig. 7a,b), but the ratio changes from season to season. The information in Figure 7 pertains to St. Paul Island for those years for which pup estimates were available on all rookeries. The ratio of pups to breeding males ranged from 29:1 in 1963 to 71:1 in 1913. At present the ratio is about 33:1. On San Miguel Island, the ratio of pups to reproductive males is about 25:1 (observed range is 10.0:1 in 1972 to 26.7:1 in 1978).

Attendance pattern

The duration of visits by females to land and the length of time spent at sea vary as the season progresses. The first visit is the longest, the last visit of the season is next longest, and those visits in between are shorter. Trips to sea become longer over the season at the rate of 1.2 days for each 30 days postpartum.

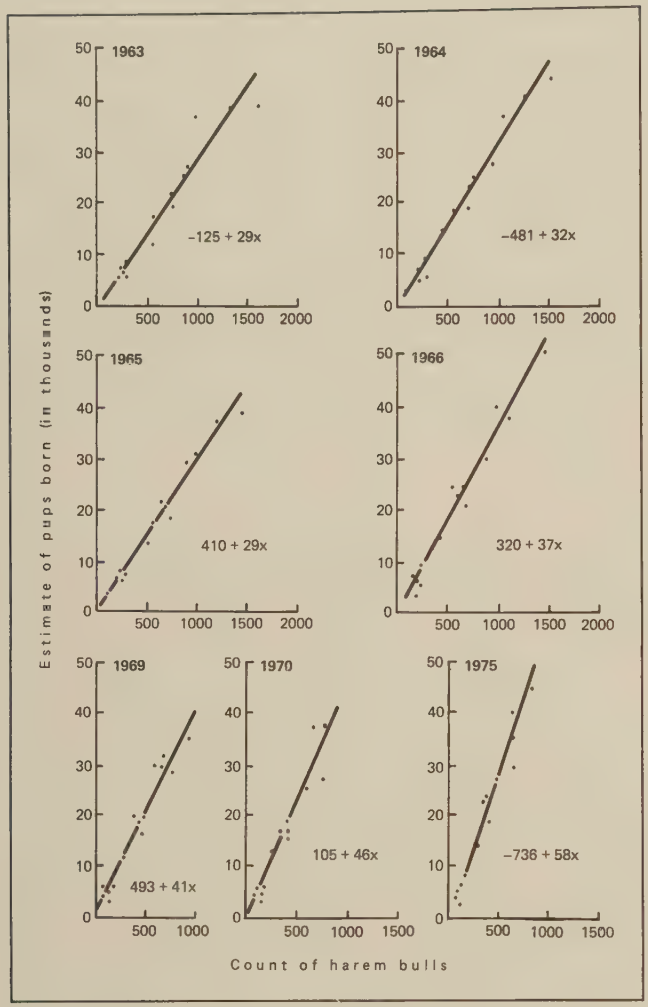


Figure 7b—Relationship of estimates of northern fur seal pups born and counts of harem bulls on the various rookeries of St. Paul Island, Alaska, 1963-75 (from York and Kozloff 1987).

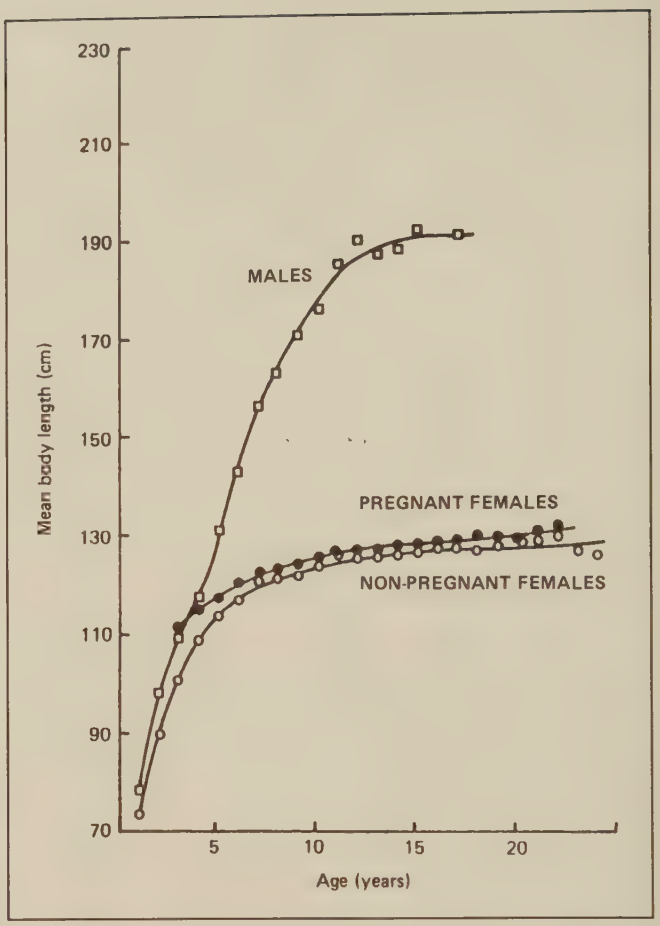


Figure 8a—Mean length, by age, of northern U.S. fur seals collected 1958-74 by Canadian and United States research vessels in the North Pacific Ocean and eastern Bering Sea (from Lander 1979b).

The following information on attendance patterns is taken from Gentry and Holt (1986) for fur seals at study sites on St. George Island:

Interval from arrival to parturition	1.2 ± 0.6 days
Mean duration of trips to sea	6.9 ± 1.4 days
Number of visits to land	8-12
Duration of first visit to land	8.3 ± 0.45 days
Duration of other visits to land	2.1 ± 0.3 days
Amount of time female available to pup	27%

GROWTH

Lander (1979b) summarized information on the growth of individual fur seals from data in the pelagic collections of Canada and the United States (1958-74). Figures 8a,b present the average lengths and weights of males and females for ages 1-25. Figures 9a,b summmarize available data on fetal growth of males and females during January-July. Mean birth weight is about 6.0 kg for males and about 5.4 kg for females. At birth, both males and females are about 60 cm in length. Full-grown adult females weigh about 40 kg and males about 150-160 kg, although at the beginning of the breeding season males may weigh as much as 180-220 kg. Typically, breeding males lose 20-25% of their mass during the breeding season (Johnson 1968).

FOOD

Kajimura (1984) and Perez and Bigg (1986) summarized the feeding information for northern fur seals in the eastern North Pacific Ocean and Bering Sea. Stomachs were collected from fur seals throughout their subarctic range by scientists from the United States and Canada during 1958-74. Kajimura characterizes the fur seal as an opportunistic feeder, preying on the most available species throughout its range.

Fifty-three species of fish and 10 species of squid were found in fur seal stomachs. Table 5 (Kajimura 1984) shows the principal forage species utilized by fur seals in the eastern North Pacific. Figures 10-12 (Kajimura 1984) summarize monthly frequency of occurrence and the volume of food in stomachs for large sampling

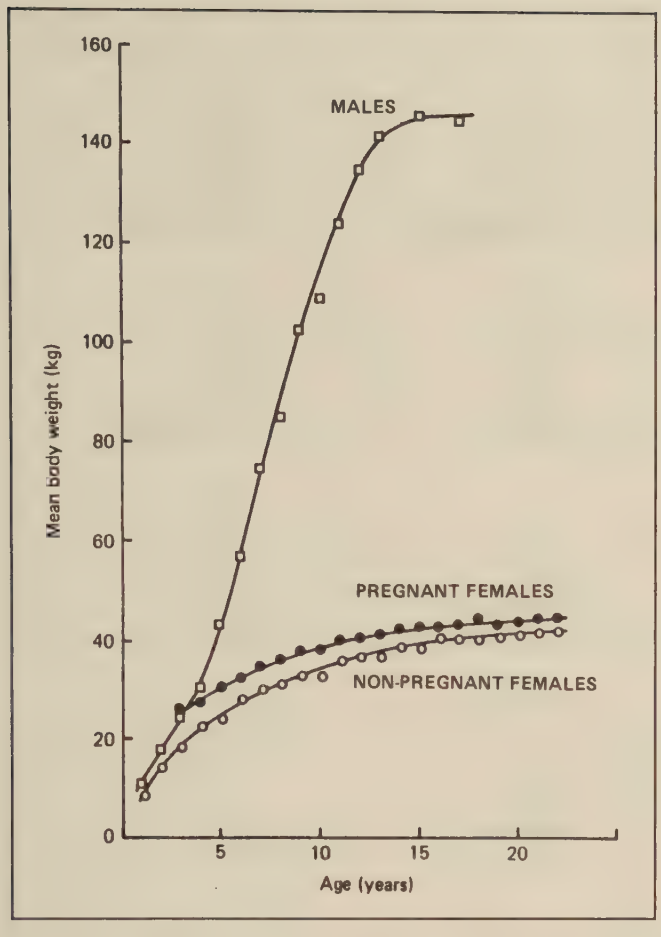


Figure 8b—Mean weight, by age, of northern fur seals collected 1958-74 by Canadian and U.S. research vessels in the North Pacific Ocean and eastern Bering Sea (from Lander 1979b).

Table 5—Principal forage species utilized by northern fur seals in the eastern North Pacific Ocean and the eastern Bering Sea, 1958-74, by area (from Kajimura 1984).

Forage species	California	Oregon	Washington	British Columbia	Gulf of Alaska	Western Alaska	Bering Sea
Fish:							
Clupea harengus passasi	—	—	x	x	x	x	x
Engraulis mordax	x	x	x	—	—	—	—
Oncorhynchus spp.	—	—	x	x	x	x	—
Mallotus villosus	—	—	x	—	x	x	x
Thaleichthys pacificus	—	—	x	x	—	—	—
Cololabis saira	x	x	—	x	—	—	—
Gadidae	—	—	—	—	—	—	x
Gadus macrocephalus	—	—	—	x	—	—	—
Merluccius productus	x	x	x	x	—	—	—
Theragra chalcogramma	—	—	—	x	x	x	x
Trachurus symmetricus	x	—	—	—	—	—	—
Sebastes spp.	x	x	x	x	x	—	—
Anoplopoma fimbria	x	—	x	x	—	x	—
Pleurogrammus monopterygius	—	—	—	—	x	x	x
Ammodytes hexapterus	—	—	—	—	x	x	x
Cephalopods:							
Loligo opalescens	x	x	—	x	—	—	—
Onychoteuthis sp.	x	x	x	—	—	—	—
Onychoteuthis borealijaponicus	—	—	—	—	x	—	—
Gonatus sp.	—	—	—	—	x	—	—
Berrytheuthis magister	—	—	—	—	x	x	x
Gonatopsis borealis	—	—	—	—	—	—	x
Unidentified squid	—	—	—	—	x	—	—

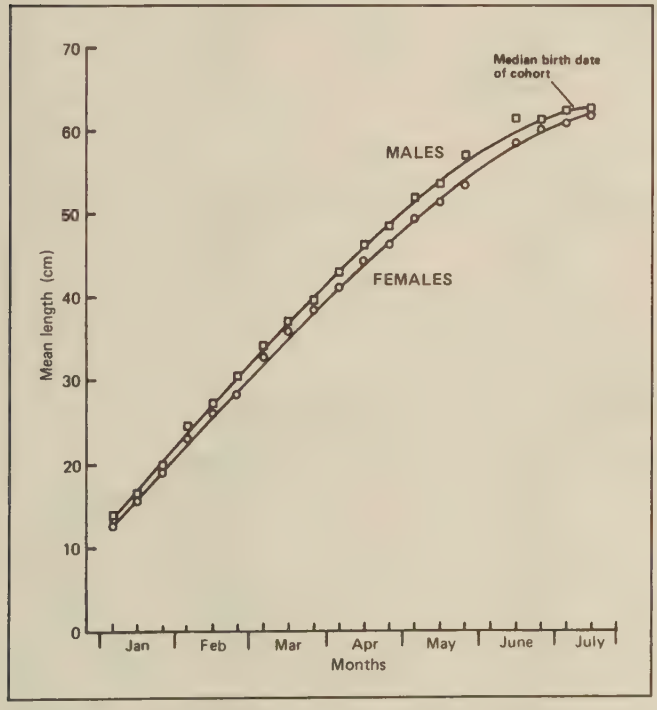


Figure 9a—Mean length of northern fur seal fetuses, by 10-day periods beginning 1 January, from 1958-74 collections by Canadian and United States research vessels in the North Pacific Ocean and eastern Bering Sea (from Lander 1979).

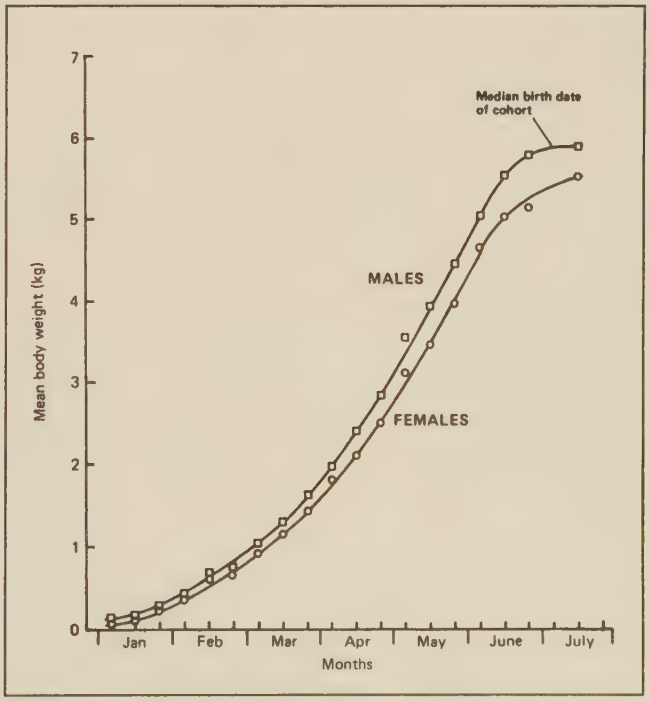


Figure 9b—Mean weight of northern fur seal fetuses, by 10-day periods beginning 1 January, from 1958-74 collections by Canadian and U.S. research vessels in the North Pacific Ocean and eastern Bering Sea (from Lander 1979).

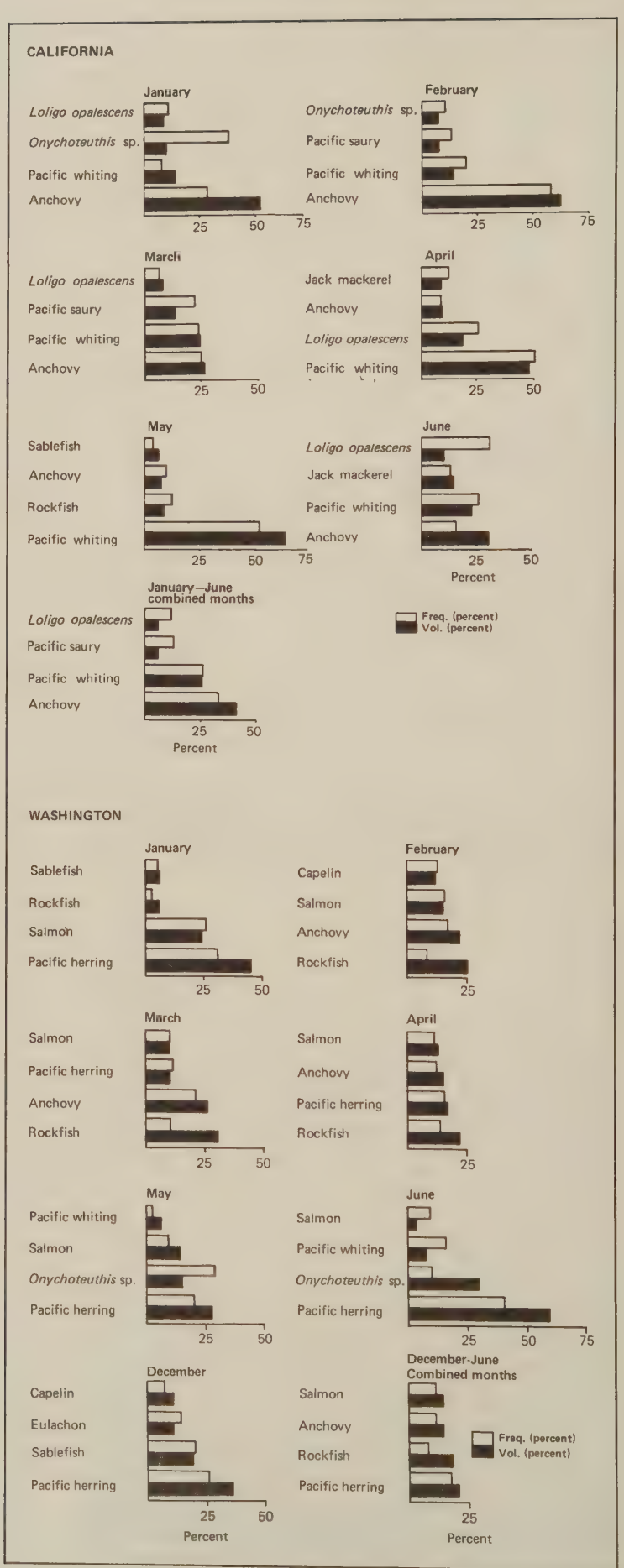


Figure 10—Principal forage species of northern fur seals off California, 1958-66 and Washington, 1958-74 (from Kajimura 1984).

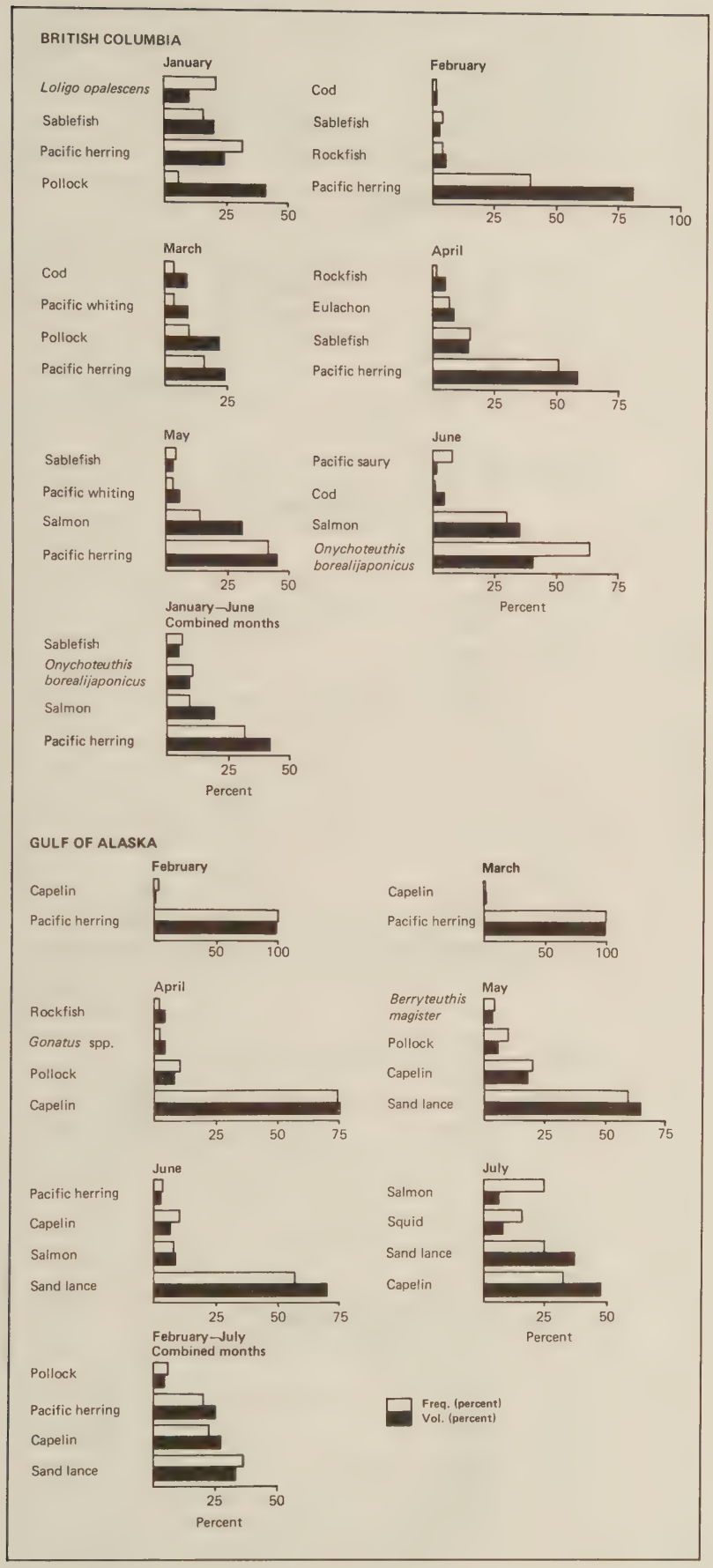


Figure 11—Principal forage species of northern fur seals off British Columbia, 1958-72, and Gulf of Alaska, 1958-68 (from Kajimura 1984).

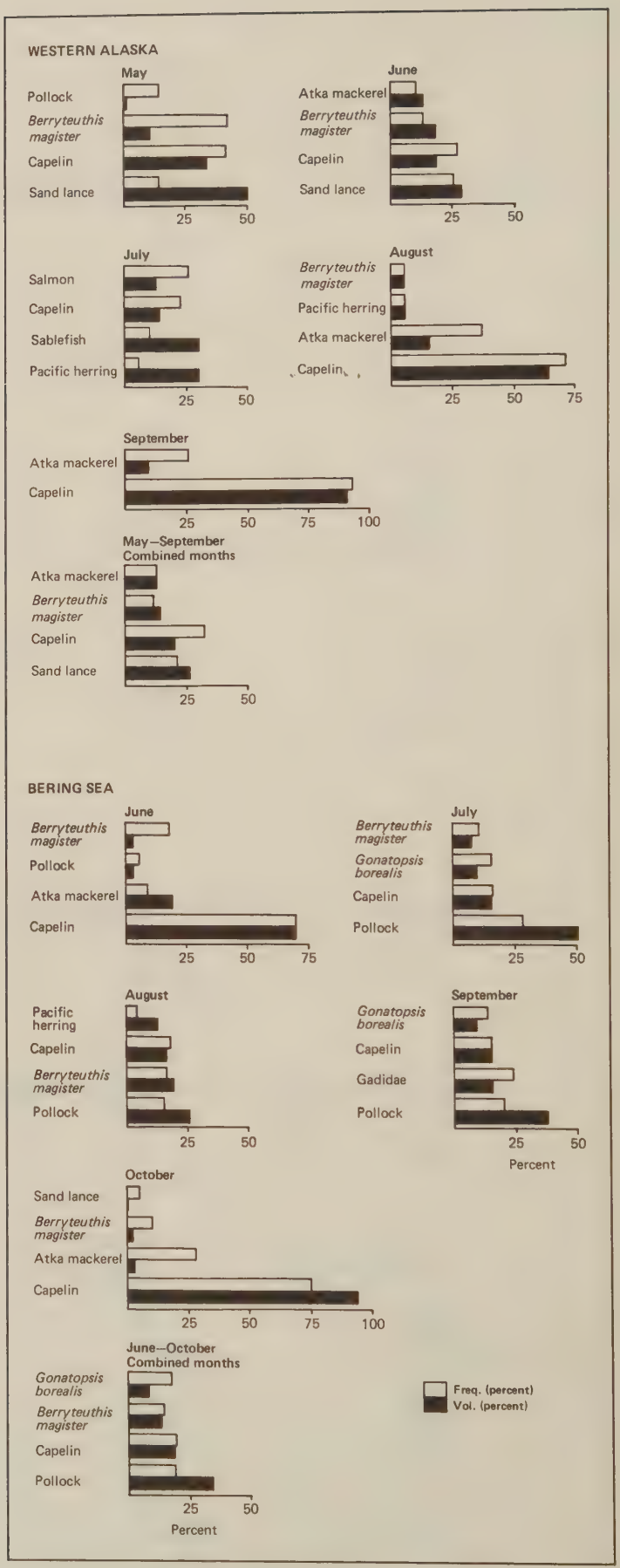


Figure 12—Principal forage species of northern fur seals in western Alaska, 1958-74, and the eastern Bering Sea, 1958-74 (from Kajimura 1984).

areas of California, Washington, British Columbia, the Gulf of Alaska, western Alaska, and the Bering Sea. In addition to the frequency of occurrence and analysis of volume of prey items, Perez and Bigg (1986) use "modified volume" and "energy adjusted modified volume" methods to describe the diet of fur seals. They characterize the fur seal diet as 60% small schooling fish, 23% other fish, and 17% squid.

CITATIONS

CHAPMAN, D. G.
1964. A critical study of Pribilof fur seal population estimates. U.S. Fish Wildl. Serv., Fish. Bull. 63:657-669.

DeLONG, R. L.
1982. Population biology of northern fur seals at San Miguel Island, California. Ph.D. thesis, Univ. Calif., Berkeley, 185 p.

FOWLER, C. W.
1982. Interactions of northern fur seals and commercial fisheries. Trans. 47th N. Am. Wildl. Nat. Resour. Conf.:278-292.

GENTRY, R. L., and J. H. JOHNSON.
1981. Predation by sea lions on northern fur seal neonates. Mammalia 45:423-430.

GENTRY, R. L., and J. R. HOLT.
1986. Attendance behavior of northern fur seals. *In* R. L. Gentry and G. L. Kooyman (eds.), Fur seals: maternal strategies on land and sea, p. 41-60. Princeton Univ. Press, Princeton, NJ.

JOHNSON, A. M.
1968. Annual mortality of territorial male fur seals and its management significance. J. Wildl. Manage. 32(1):94-99.

KAJIMURA, H.
1984. Opportunistic feeding of the northern fur seal, *Callorhinus ursinus*, in the eastern North Pacific Ocean and eastern Bering Sea. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-779, 49 p.

KENYON, K. W., V. B. SCHEFFER, and D. G. CHAPMAN.
1954. A population study of the Alaska fur seal herd. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Wildl. 12, 77 p.

KOZLOFF, P. (editor).
1980. Fur seal investigations, 1979. NWAFC Processed Rep. 80-4, 93 p. Natl. Mar. Mammal Lab., Northw. Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115-0070.
1982. Fur seal investigations, 1981. NOAA Tech. Memo. NMFS F/NWC-37, Natl. Mar. Mammal Lab., Northw. Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115-0070, 88 p.

LANDER, R. H.
1975. Method of determining natural mortality in the northern fur seal (*Callorhinus ursinus*) from known pups and kill by age and sex. J. Fish. Res. Board Can. 32:2447-2452.
1979a. Role of land and ocean mortality in yield of Alaska fur seals. Fish. Bull., U.S. 77:311-314.
1979b. Fur seal growth. *In* H. Kajimura, R. H. Lander, M. A. Perez, A. E. York, and M. A. Bigg (eds.), Preliminary analysis of pelagic fur seal data collected by the United States and Canada during 1958-1974, p. 143-157. Unpubl. manuscr. Natl. Mar. Mammal Lab., Northw. Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115-0070. (Submitted to the Standing Scientific Committee, 22nd Annual Meeting of the North Pacific Fur Seal Commission, 2-6 April 1979, Wash., D.C.
(editor). 1980. Summary of northern fur seal data and collection procedures. Vol. 1: Land data of the United States and Soviet Union (excluding tag and recovery records). NOAA Tech. Memo. NMFS F/NWC-3, Natl. Mar. Mammal Lab., Northw. Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115-0070, 315 p.
1981. A life table and biomass estimate for Alaskan fur seals. Fish. Res. (Amst.) 1(1):55-70.

LANDER, R. H., and H. KAJIMURA.
1982. Status of northern fur seals. *In* Mammals in the seas. 4, FAO Fish Ser. 5, Vol. 4:319-345.

LLOYD, D. S., C. P. McROY, and R. H. DAY.
1981. Discovery of northern fur seals (*Callorhinus ursinus*) breeding on Bogoslov Island, southeastern Bering Sea. Arctic 34(4):318-320.

LOUGHLIN, T. R.
1985. A new northern fur seal rookery, Bogoslof Island, Alaska. *In* P. Kozloff (ed.), Fur seal investigations, 1983, p. 42-43. Tech. Memo. NMFS F/NWC-78, Natl. Mar. Mammal Lab., Northw. Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115-0070.

LOUGHLIN, T. R., L. CONSIGLIERI, R. L. DeLONG, and A. T. ACTOR.
1983. Incidental catch of marine mammals by foreign fishing vessels, 1978-81. Mar. Fish. Rev. 45(7-9):44-49.

PEREZ, M. A., and M. A. BIGG.
1986. Diet of northern fur seals, *Callorhinus ursinus*, off western North America. Fish. Bull., 84:959-973.

PETERSON, R. S.
1968. Social behavior in pinnipeds with particular reference to the northern fur seal. *In* R. J. Harrison, R. C. Hubbard, R. S. Peterson, C. E. Rice, and R. J. Schusterman (eds.), The behaviour and physiology of pinnipeds, p. 3-53. Appleton-Century-Crofts, N.Y., 411 p.

ROPPEL, A. Y.
1984. Management of northern fur seals on the Pribilof Islands, Alaska, 1786-1981. U. S. Dep. Commer., NOAA Tech. Rep. NMFS 4, 26 p.

SCHEFFER, V. B., C. H. FISCUS, and E. I. TODD.
1984. History of scientific study and management of the Alaska fur seal, *Callorhinus ursinus*, 1786-1964. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-780, 70 p.

YORK, A. E.
1980. Pregnancy rates and migration. *In* H. Kajimura, R. H. Lander, M. A. Perez, A. E. York, and M. A. Bigg (eds.), Further analysis of pelagic fur seal data collected by the United States and Canada during 1958-1974, Part 1, p. 58-63. Unpubl. manuscr. Natl. Mar. Mammal Lab., Northw. Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115-0070. (Submitted to Standing Scientific Committee, North Pacific Fur Seal Commission, 7-11 April 1980, Moscow, USSR.)
1983. Average age at first reproduction of the northern fur seal (*Callorhinus ursinus*). Can. J. Fish. Aquat. Sci. 40(2):121-127.

YORK, A. E., and J. R. HARTLEY.
1981. Pup production following harvest of female northern fur seals. Can. J. Fish. Aquat. Sci. 38(1):84-90.

YORK, A. E., and P. KOZLOFF.
1987. On the estimation of numbers of northern fur seal, *Callorhinus ursinus*, pups born on St. Paul Island 1980-86. Fish. Bull., U.S. 85:367-375.

Galapagos Fur Seal, *Arctocephalus galapagoensis*[1]

FRITZ TRILLMICH
Max-Planck-Institute für Verhaltensphysiologie
Abteilung Wickler
D-8131 Seewiesen
W-Germany

INTRODUCTION

When Clark (1975) published a species summary about the Galapagos fur seal, *Arctocephalus galapagoensis*, little was known about its natural history. It was still believed to be very rare, and Orr (1972) described it as in the "danger zone." Available knowledge was mostly on skull anatomy (Repenning et al. 1971) and thus did not allow many comparisons with the more temperate species of the genus. Since then, much information has become available through recent work which began in 1976. The information given in this review necessarily overlaps somewhat with a previous description of the natural history of the species (Trillmich 1984); however, I have tried to make it complementary. The references give a complete list of original contributions to our knowledge about the Galapagos fur seal, omitting most publications which merely gathered or reinterpreted old data.

METHODS

The recent studies of the Galapagos fur seal were all made at Cabo Hammond (long. 91°37′W, lat. 0°28′S), which is the southwest corner of Fernandina, the westernmost island of the Galapagos Archipelago. Fernandina is uninhabited and free of introduced larger organisms. A continuous 530-m section of coastline was the main study area, and most behavioral observations were made along an approximately 180 m subsection of it. Since the study site is part of the Galapagos National Park, killing of animals is entirely prohibited, thus precluding sampling programs for the determination of age structure, pregnancy rates, and so on.

The seals were studied from 1976 onwards. Visits to the study area took place between August and November in 1977 and 1979-83. Shorter periods were spent on Cabo Hammond in August and December 1976, February and June 1978, and April 1981. D. Limberger carried out observations almost continuously at Cabo Hammond between August 1982 and March 1983, during the recent strong El Niño. Observations were always made by sitting or moving quietly between the animals, without the use of a hide. Even territorial males usually became oblivious to our presence after a few hours habituation.

From 1979 we tagged Galapagos fur seals with flexible, UV-resistant Allflex sheep ear tags applied to the trailing edge of the front flipper. If they survive the first month on the animal, these tags last very well. Pups were weighed with spring balances (to the nearest 50 g) or an electronic scale (to the nearest 5 g). Adults were induced to move onto a board placed between bathroom scales and were weighed in this manner without handling. A few captured adult females were weighed with spring balances.

HARVESTING

The Galapagos fur seal was hunted, apparently indiscriminately, during the 19th century. Sealing in the Galapagos was carried mainly out by whalers while calling into the Galapagos to pick up fresh water or provisions (e.g., giant tortoise meat); but some sealers apparently hunted the seals professionally, since the largest documented catch for one voyage was 8,000 animals (Captain Fanning in 1816, according to Townsend 1934). Townsend (1934) provided a list of 22,508 skins taken in the Galapagos between 1816 and 1933. He considered it incomplete since it included only the harvest of ships sailing from California. English and Spanish vessels

[1]Contribution No. 378 of the Charles Darwin Foundation.

are also known to have come to the Galapagos for sealing (Slevin 1959), but their catches have not been documented.

By 1898-99 the number of fur seals had been reduced so much that no well-defined rookeries could be found during a 6-month stay in the Galapagos by the Hopkins Stanford Galapagos Expedition (Heller 1904). Nevertheless, 224 skins were collected during this expedition, and Heller mentions that the captain of his ship had had about the same success in several previous years (a statement not accounted for in Townsend's (1934) list and thus attesting to its incompleteness, even for ships sailing from California). When the schooner *Academy* spent a year in Galapagos waters between 1905 and 1906 making collections for the California Academy of Sciences, only one Galapagos fur seal was taken (on Genovesa). Around that time the population was probably at an all-time low. As sealing became totally uneconomical, interest waned and there is no record of later sealing expeditions. The next report of a Galapagos fur seal came from Banning (1933) who observed fur seals on Genovesa during the Hancock expeditions of 1932 and 1933 which brought back eight specimens to the San Diego Zoo (Townsend 1934).

Since the 1940s, Galapagos fishermen have known about sizeable fur seal colonies on Pinta and Marchena (F. Angermeyer, Galapagos inhabitant, pers. commun.). In 1957 Eibl-Eibesfeldt (1959) discovered a colony on Santiago which he estimated at about 100 animals. Between 1960 and 1962 Leveque (1963) made a partial survey of the Galapagos coasts and found colonies on Santa Cruz, Baltra, North Seymour, Rabida, north Santiago, northeast and north Isabela, Genovesa, Marchena, Wolf, and Darwin. His actual counts gave a total of 1,940 fur seals, but he tentatively estimated a population size of 4,000 animals.

It is impossible to decide whether the apparent increase in fur seal numbers since 1940 is due to an actual increase in numbers or to an increase of visits to the rather inaccessible habitat of the Galapagos fur seal. We may tentatively assume that the species has been recovering and perhaps even extending its range since about 1910. It was helped a little in 1934 when the Ecuadorian government prohibited all hunting of native Galapagos animals. However, the legislation was impossible to enforce and consequently had little effect on the local residents, although it may have deterred foreigners. Then, in 1959, over 80% of the Galapagos archipelago was declared a National Park, and subsequent protection of the fur seal has been successful.

POPULATION SIZE AND TRENDS

The earlier estimates of population size (about 4,000 according to Leveque 1963; more than 1,000 according to Orr 1972, who does not discuss Leveque's estimate but cites the article) were necessarily guesses based on very incomplete surveys of the Galapagos coastline and virtually no knowledge of the animals' behavior. Thus they cannot be used for an assessment of population trends or changes in the distribution of the species.

An almost complete population census was made in 1977-78 during April, May, and June. Most counting was carried out from an inflatable rubber boat slowly cruising close inshore. On the few occasions possible, censuses were made on foot and, at a few places, from a small fishing boat cruising at a speed of 2-3 kn. Comparison proved that counting on foot was the most reliable method.

The total number of fur seals counted was 9,785. By applying corrections for the method of counting and the phase of the lunar month at the time of counting (Trillmich and Mohren 1981), an estimate of 30,000 fur seals was derived (Trillmich unpubl. data). About one-third of them live on Isabela, the largest of the Galapagos islands (Trillmich 1984). Approximate population size per island is given in Table 1. Figure 1 summarizes the present distribution of the Galapagos fur seal.

Table 1—Population size of the Galapagos fur seal by islands. Numbers estimated from direct counts by correcting for census method and lunar phase and given to the nearest 50 fur seals.

Island	Estimated number
Baltra	200
Darwin	100
Fernandina	2,400*
Floreana	50
Genovesa	1,250
Isabela	12,000*
Marchena	2,350
Pinta	3,850
Pinzon	100
Rabida	400
San Cristobal	50
San Salvador	2,350
Santa Cruz	1,100
Seymour-N	300
Wolf	600
Total	27,100

*Incomplete census.

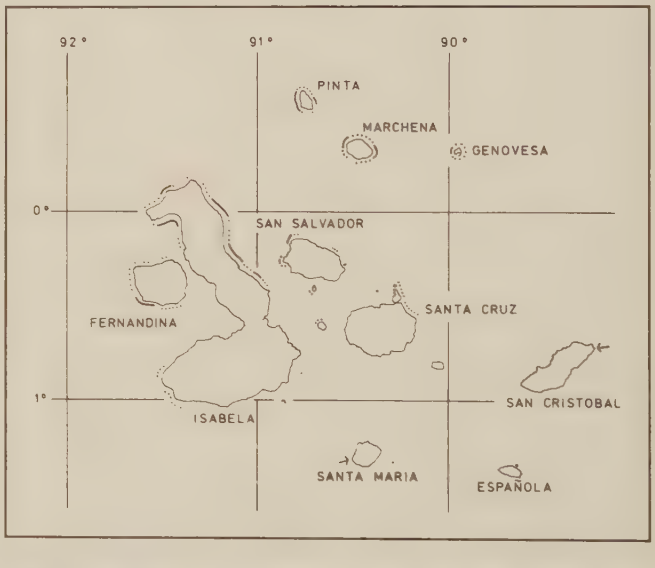


Figure 1—Distribution of the Galapagos fur seal. Dotted lines indicate sparse colonies; continuous lines indicate dense colonies. Arrows indicate hauled-out animals, presumably no breeding.

Colonies occur mostly on the western shores of the islands, where upwelling is strongest due to steep slopes of the submarine flanks of the volcanic islands. Perhaps such areas of upwelling are particularly rich in prey species, but no relevant data on their distributions are available.

The population at the main study site, Cabo Hammond, remained stable between 1977 and 1982. However, the strong El Niño of

1982-83 killed at least the three youngest year classes and also adversely affected the survival of adult males (Trillmich and Limberger 1985).

INFLUENCES

It is not yet clear whether the population is close to carrying capacity or still recovering from its earlier exploitation because of the limited time span over which we have reliable data; consequently I can only speculate on factors which may influence population size.

A density-dependent limiting factor may be competition between females on land for shaded pupping sites (Trillmich 1984). Another important, and presumably density-independent, factor limiting population size may be food, as several year classes perished completely during the recent El Niño, apparently from food shortage.

COMPETITORS

Competition with the sympatric Galapagos sea lion, *Zalophus californianus wollebaeki*, is, at present population densities, very limited on land since the species differ in habitat preference: fur seals choose rocky shores with steep broken relief, while sea lions choose wind-exposed beaches, whether sandy or rocky. At sea, the differences in their feeding behavior reduce interactions: sea lions dive relatively deep during the daytime and the fur seals much shallower at night (Kooyman and Trillmich 1986 a,b). Furthermore, preliminary analysis of food remains in scats and vomits shows that both species feed mostly on different fish species and that only the fur seals take a considerable amount of cephalopod prey (Clarke and Trillmich 1980; Trillmich unpubl. data).

PREDATORS

Sharks may cause considerable mortality as fur seals with large shark bites were often observed. Since it is impossible to determine the proportion of fatal attacks by sharks, this cause of mortality cannot be quantified at present. However, among a sample of 83 marked females observed for at least 3 months during a reproductive season, none were recorded as lost and this indicates that shark predation is not a major cause of adult mortality. On one occasion killer whales, *Orcinus orca*, were seen to hunt cooperatively and actually kill a Galapagos fur seal in front of the study colony.

Introduced feral dogs are the only alien predators which present a potentially serious threat to a large subpopulation of fur seals on Isabela. They were observed killing pup fur seals and attacking adults. Fortunately, large feral dogs were present only on southern Isabela where they exterminated most of the fur seal population. The present dog eradication program of the Galapagos National Park has apparently brought this problem under control. Just how permanent that will be is hard to guess; unfortunately, a small population of feral dogs which still exists in the highland areas of Cerro Azul and Sierra Negra could re-invade coastal areas.

MORTALITY

Mortality of all age groups varied widely between years due to extreme fluctuations in the environment during the study. For example, 1981 was an especially good year for the fur seals, while 1976 contained a weak El Niño and 1982-83 a catastrophic one which caused 100% pup mortality (Limberger et al. 1983). The values in Table 2 were calculated by excluding the year 1982-83. They are, therefore, a biased sample of the available data, but presumably are closer to long-term average conditions than if the 1982-83 data had been included.

Table 2—Mortality estimates for Galapagos fur seals.

Age class	*N*	Mortality	Remarks
Birth-30 days	202	9%	Pups without sibling
Birth-30 days	268	15%	Including pups with older siblings
Adult females	60	15%	Per year, females with pups only
Territorial males	22	32%	Per year

Table 2 gives two separate estimates of pup mortality during the first month of life because females are still accompanied by their older offspring in about 8% of all births. In these cases mortality of newborn offspring due to competition with older siblings is very high and thus is a very important mortality factor which does not exist for most other *Arctocephalus* species. Adult female mortality was estimated for females with pups only, since they are the most sedentary subset of the female population and are most likely to be found in subsequent seasons. Nevertheless, the value given in Table 2 may still overestimate female mortality because it does not take into account dispersal of females with yearlings away from the main pupping sites.

REPRODUCTIVE PARAMETERS

Because the tagging program only began in 1979 and the killing of Galapagos fur seals is totally prohibited by the National Park authorities, very few data on age-specific reproductive parameters are currently available.

The youngest tagged female seen copulating was 3 years old. Estimating age from size (a very dubious method), it appeared that most pupping females were aged 5 years or older. Age-specific fecundity of females is unknown.

Fully grown males found dead during or towards the end of the reproductive season were aged from longitudinal sections of canine teeth. Presumably most of them had been territorial before death since they were badly scarred. One of these males was observed holding a territory in the month before his death. Their ages ranged from 9 to $\geq$11 years (n=14). Condylobasal length of their skulls varied between 198 and 212 mm. The data suggest that males usually attain territorial status at 8-10 years of age.

REPRODUCTIVE ECOLOGY

Pupping

The pupping period begins in mid-August and lasts until mid-November. It peaks at slightly different times each year, between the last week of September and the first week of October. In 1979 and 1980 all pups born in the study area were marked within 4 days of birth. Along a 530-m coastline, 162 pups were born in 1979 and 228 in 1980, with 90% of the births occurring between 17 August and 29 October in 1979 and 27 August and 29 October in 1980, i.e., over about 70 days. Births peaked on 3 October and 26 September, respectively.

Density on land was always highest shortly before and during a full moon (Trillmich and Mohren 1981; Trillmich 1986a) and declined sharply thereafter. The highest densities in suitable pupping habitat were about 4 females per 100 m^2 around full moon. Density dropped to approximately 1.6 females per 100 m^2 around the time of the new moon. Nearest neighbor distances were rarely lower than about 0.5 m, but no systematic records were made of them because the very broken habitat of the seal meant it was often unclear whether nearest neighbors were aware of each other. Distances between fur seals resting ashore during the warmest hours of the day were mostly determined by the distribution of resting sites in the shade.

Weaning

The period of dependence of young in the Galapagos fur seal is unusually long. They are attended and suckled regularly until about 2 years old or older. Yearlings are not weaned at the birth of a new pup but compete with their siblings for their mother's milk. Usually the younger pup, although initially defended by its mother, quickly loses in this competition and starves to death within a month or less. The same occurs in many cases when mothers of dependent 2-year-olds give birth to a new pup. Only in exceptional cases do mothers succeed in raising a 2-year-old and a newborn pup simultaneously (Trillmich 1986a).

Over three seasons, we studied how lactating female Galapagos fur seals apportioned their time. Females stayed with the newborn for approximately 7 days after birth and then returned to a normal routine of alternating foraging trips and periods ashore attending the pup. They foraged almost exclusively at night, their trips being longest (50-70 hours) around the new moon or decreasing half moon and shortest around the full moon (10-20 hours). Periods ashore followed the reverse pattern. Young were nursed until about 2 years old. Mothers of yearlings spent less time ashore than mothers of young pups (10 days to three months) by making more foraging trips per unit time, but individual trips were of roughly equal duration for both groups of mothers. Nursing time increased with age of the young, reaching a maximum of 70-80% of attendance time in mothers of yearling males. A rough estimate of total maternal effort for raising one offspring would be 300 foraging trips and 3,000 hours of nursing (Trillmich 1986a).

Territoriality

Due to the Galapagos fur seal's long pupping season, no territorial male is able to maintain his territory for the whole season. The longest territory tenure was 51 days. About 30% of the males returned to their previous territory within the same season and were territorial for a second time. The median time of first territory tenure was 27 days and 15 days in the second (Trillmich 1984).

Parallel observations on territorial bulls and pup production exist for different subsections of the study area for 4 years. The largest sample (1980) showed that there were 39 territorial bulls on the area where 147 pups were born, i.e., 3.8 pup births per bull. Combined data from the main study site in 1977, 1979 and 1981 showed 86 births per 24 bulls or 3.6 births per bull. There are two problems with accepting these figures as a relevant estimate of the degree of polygyny in the Galapagos fur seal: (1) The distribution of territory tenure times and, consequently, of the number of copulations achieved is very skewed (Fig. 2); and (2) there is a considerable number of copulations with females who have yearlings, 2-year-olds, or no pups at all, and these clearly represent a large proportion of all copulations. This unusual situation occurs because females care for their pups for about 2 years, and pregnancy rates are greatly reduced during this time (Trillmich 1986b).

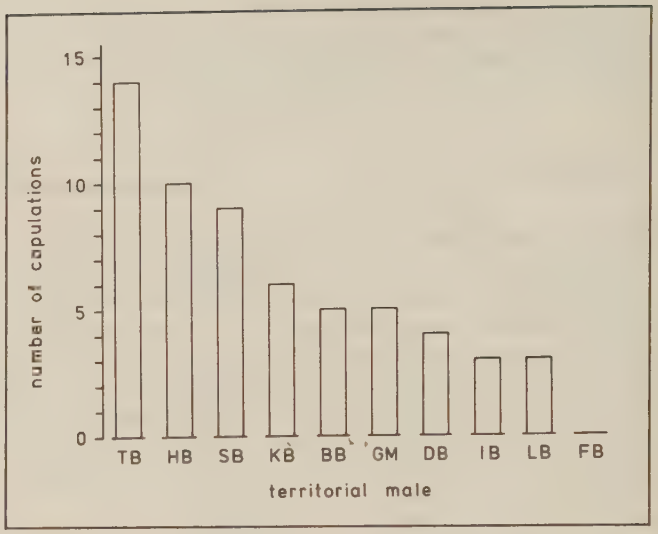


Figure 2—Copulatory success of territorial bulls in the study area in 1977.

Table 3—Weights (kg) of Galapagos fur seals.

Age	*N*	Weight (mean ± sd)
Newborn	23	3.6 ± 0.35
6 months	131	9.0 ± 1.3
12 months	56	11.3 ± 2.2
24 months	32	14.7 ± 2.7*
Adult female	10	27.3 ± 3.3
Adult male	3	63.7

*Sample presumably biased towards low weights.

The best available estimates derive from the proportion of observed copulations of females who have pups compared with those of females with yearlings, older young, or no offspring. These figures indicate that about 30-50% of all copulations are with females who have not pupped in the current pupping season. This would give an estimate of 5-7 copulations per bull per season.

GROWTH

The data available on the growth of the Galapagos fur seal are summarized in Table 3. Weaning weights are presumably slightly higher than the weight given in Table 3 for 2-year-olds. Growth rates of pups over the first 2 months of life were 58 g/day for males and 43 g/day for females (Trillmich 1986b).

Townsend (1934) gave the weight of an eviscerated carcass of a full grown male as 50.3 kg. Assuming eviscerated weight to be around 75% of live weight, this would correspond to 67 kg. Trillmich (1984) obtained three weights of live territorial males ranging from 60 to 68 kg. Adult females were found to weigh between 21.5 and 33.0 kg with a mean of 27.3 kg. Curvilinear body length

was 152 cm for territorial males and 120 cm for adult females (Trillmich 1984). These results are similar to Townsend's (1934) measurements of his adult male, which was 137 cm from the tip of its nose to the tip of its tail, and to Heller's (1904) measurements which give an average adult male length of 157.1 cm ($n=5$) and an average adult (?) female length of 102.5 cm ($n=2$). The data on weight and size clearly show that this species is by far the smallest fur seal.

FOOD

Very little information is presently available on the diet of the Galapagos fur seal. Clarke and Trillmich (1980) give a list of cephalopods identified from vomits of adult female fur seals collected in 1976 and 1977. *Onychoteuthis banksi*, having a mean weight of 12 g, comprised 74% of the biomass in the sample. In a later sample (1981; M. R. Clarke, Mar. Biol. Assoc. U.K., Plymouth, unpubl. data), ommastrephids comprised 84% of all squid beaks found. A large collection of otoliths from scats (approximately 3,000) was made in 1983 and is presently being analysed. Because the scats contained very few squid beaks and the vomits no otoliths, it is clear that these items are eliminated in a different manner, thus making it impossible to comment on the relative dietary importance of squid and fish as food.

ACKNOWLEDGMENTS

I would like to thank the Parque Nacional Galapagos and the Charles Darwin Research Station for permission to work at Fernandina Island and for their support during the field work. This study was supported by the Max-Planck-Gesellschaft, and I am greatly indebted to W. Wickler for his continuous support.

CITATIONS

BANNING, G. H.
1933. Hancock expedition of 1933 to the Galapagos Islands; general report. Bull. Zool. Soc. San Diego 10:1-30.

CLARK, T. W.
1975. *Arctocephalus galapagoensis*. Mammalian species no. 64. Am. Soc. Mammal.

CLARKE, M. R., and F. TRILLMICH.
1980. Cephalopods in the diet of fur seals of the Galapagos Islands. J. Zool. (Lond.) 190:211-215.

EIBL-EIBESFELDT, I.
1959. Survey on the Galapagos Islands. UNESCO Mission Rep. 8, Paris.

HELLER, E.
1904. Mammals of the Galapagos Archipelago, exclusive of the Cetacea. Proc. Calif. Acad. Sci., Ser. 3, 3:233-250.

KOOYMAN, G. L., and F. TRILLMICH.
1986a. Diving behavior of Galapagos fur seals. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur Seals: Maternal strategies on land and at sea, p. 186-195. Princeton Univ. Press.
1986b. Diving behavior of Galapagos sea lions. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur Seals: Maternal strategies on land and at sea, p. 209-219. Princeton Univ. Press.

LEVEQUE, R.
1963. Le statut actuel des vertebres rares et menaces de'l archipel des Galapagos (The current status of rare and endangered vertebrates of the Galapagos Islands). Terre Vie 110:397-430.

LIMBERGER, D., F. TRILLMICH, G. L. KOOYMAN, and P. MAJLUF.
1983. Reproductive failure of fur seals in Galapagos and Peru in 1982-83. Trop. Ocean-Atmos. Newsletter 21:16-17.

ORR, R. T.
1972. Galapagos fur seal (*Arctocephalus galapagoensis*). *In* Seals. Proc. of a working meeting of seal specialists on threatened and depleted seals of the world. IUCN Morges 1972, p. 124-128.

REPENNING, C. A., R. S. PETERSON, and C. I. HUBBS.
1971. Contributions to the systematics of the southern fur seals, with particular reference to the Juan Fernandez and Guadalupe species. *In* Burt, W. H. (ed.), Antarctic Pinnipedia. Antarctic Research Series, Vol. 18:1-34. Am. Geophys. Union, Wash., D.C.

SLEVIN, J. R.
1959. The Galapagos Islands. A history of their exploration. Occas. Pap. Calif. Acad. Sci. 25, 150 p.

TOWNSEND, C. H.
1934. The fur seal of the Galapagos islands. Zoologica (N.Y.) 18:43-56.

TRILLMICH, F.
1981. Mutual mother-pup recognition in Galapagos fur seals and sea lions: cues used and functional significance. Behaviour 78:21-42.
1984. The natural history of the Galapagos fur seal, *Arctocephalus galapagoensis* Heller. *In* Perry, R. (ed.), Key environments: Galapagos. Pergamon Press, Oxford.
1986a. Attendance behavior of Galapagos fur seals. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur Seals: Maternal strategies on land and at sea, p. 196-208. Princeton Univ. Press.
1986b. Maternal investment and sex-allocation in the Galapagos fur seal, *Arctocephalus galapagoensis*. Behav. Ecol. Sociobiol. 19:157-164.

TRILLMICH, F., and D. LIMBERGER.
1985. Drastic effects of El Niño on Galapagos pinnipeds. Oecologia (Berl.) 67:19-22.

TRILLMICH, F., and W. MOHREN.
1981. Effects of the lunar cycle on the Galapagos fur seal, *Arctocephalus galapagoensis*. Oecologia (Berl.) 48:85-92.

South American Fur Seal, *Arctocephalus australis*, in Uruguay

RAUL VAZ-FERREIRA
Departamento de Zoologia de Vertebrados
Facultad de Humanidades y Ciencias
Tristan Narvaja 1674
Montevideo, Uruguay

ALBERTO PONCE DE LEON
Departamento de Oceanografia
Facultad de Humanidades y Ciencias
Tristan Narvaja 1674
Montevideo, Uruguay

HISTORY OF HARVESTING

According to Vaz-Ferreira (1950, 1976a,b, 1982) and Ponce de Leon (1983a), the exploitation of fur seals in Uruguay began shortly after the discovery of the country by Juan Diaz de Solis in 1515, whose mates, after his death, took a cargo of fur seal skins to be sold in Seville. The next mention of commercial exploitation is from 1724, the year in which seal oil was used for illumination of the city of Maldonado. In 1792 exploitation was begun by the Real Compania Maritima on instructions of the King of Spain, and continued until the English invasion of the territory in 1808. After that, harvesting was done by concessionaries under the government's control.

As described by Vaz-Ferreira (1950), sealing has been conducted on all the islands populated by the species: Isla de Lobos and Islote de Lobos off Punta del Este, and Marco, Encantada, Rasa, and Islote near Cabo Polonio.

Some data exist for the fur seal harvest between 1873 and 1900 (Table 1), relying chiefly on the accounts of Veritas (1895) and the Bering Sea Tribunal of Arbitration (1895). These give a total of 438,445 and a mean annual catch of 15,659 pelts, apparently sustained for at least 28 years. No records from 1901 to 1909 are available. The catch for 1910-42 was 71,955 fur seals, according to Perez-Fontana (1943). (Apparently no killing occurred, or no records are available, for 1913, 1915, 1917-18, 1930-33, and 1938-39.) From 1943 to 1947 a total of 17,000 seals was taken. In 1948 and 1949 there was no killing, and a management project was started. In 1950 the harvest at Isla de Lobos was restricted exclusively to males, and 1,692 pelts were obtained. Between 1959 and 1983 a total of 224,793 seals were taken (Table 2), averaging 8,990 per year. The reduction in 1982 and 1983 was due chiefly to a significant drop in demand by the market.

Table 1—Harvest (number of pelts taken) of fur seals in Uruguay, 1873-1900.

Year	Harvest	Year	Harvest	Year	Harvest
1873	8,190	1883	12,843	1892	15,870
1874	9,449	1884	14,872	1893	17,779
1875	9,204	1885	12,247	1894	20,763
1876	11,353	1886	17,072	1895	17,421
1877	13,066	1887	17,788	1896	23,639
1878	14,493	1888	21,150	1897	19,234
1879	14,093	1889	15,700	1898	17,685
1880	16,382	1890	20,150	1899	17,235
1881	14,473	1891	13,871	1900	18,828
1882	13,595				

Table 2—Harvest of fur seals in Uruguay, 1959-83.

Year	Lobos Island and Islote	Cabo Polonio Islands	Total
1959	5,679	2,430	8,109
1960	4,562	—	4,562
1961	5,003	—	5,003
1962	5,113	—	5,113
1963	4,700	2,300	7,000
1964	5,917	2,058	7,975
1965	5,070	2,055	7,125
1966	6,000	3,500	9,500
1967	7,000	2,942	9,942
1968	7,421	3,531	10,952
1969	7,857	3,573	11,430
1970	8,390	3,550	11,940
1971	8,248	4,406	12,654
1972	8,122	3,614	11,736
1973	7,480	3,817	11,297
1974	8,370	3,770	12,140
1975	8,705	3,902	12,607
1976	9,793	4,252	14,045
1977	6,870	4,063	10,933
1978	6,844	3,680	10,524
1979	6,929	3,567	10,496
1980	—	—	9,320
1981	8,215	—	8,215
1982	1,375	—	1,375
1983	300	500	800

The management and exploitation of the Uruguayan herds from 1950 to 1975 was by Servicio Oceanografico y de Pesca (SOYP). This was restructured in 1975 and divided into the Instituto Nacional de Pesca (INAPE) and Industria Lobera y Pesquera del Estado (ILPE), the latter responsible for control and exploitation of the fur seals. The pelts are processed by a plant belonging to the same institution, and is now one of the few in the world doing this kind of processing. Oil from fur seals is obtained on Isla de Lobos and Cabo Polonio from the seals killed on nearby islands. Genitals of adult males are exported to countries in Asia. Teeth have a small local market for use in handicrafts.

POPULATION SIZE AND TRENDS

Data for 1953 are summarized in Table 3. In subsequent years the number of pups born has risen steadily, and the breeding seals are occupying a greater area. The total estimated population was 129,000 in 1960, 174,000 in 1965, and 252,000 in 1972 (Ximenez 1973).

In 1981, a total of 14,815 pups were counted at Isla de Lobos (Vaz-Ferreira et al. 1985) in contrast to 7,460 in 1956. Thus numbers doubled from 1956 to 1981. The pup censuses of 1956 and 1981 were made in early February when births of *A. australis* and the South American sea lion *Otaria flavescens* were finished, and it was possible to walk throughout the island. Adult seals were chased away, but pups remained or went briefly into the water and could easily be counted directly. The few which remained in crevices were counted separately. Since counts are made when pups are already 1 or 2 months old, this kind of census is valid only for years in which no big storms occur causing substantial early pup mortality.

The 1953 adult census was made in January by photographing the islands from elevated points and counting the seals on the pictures.

Table 3—Counts of pups and adults of the South American fur seal in Uruguay.

Group	Islands	Pups 1953[a]	Pups 1956[a]	Adults 1953[b]
Lobos	Lobos	4,435	7,460	10,578
	Islote	500		500
Torres	Rasa	15	178	1,599
	Encantada	2,128	2,383	1,400
	Islote	280	337	667
Castillos	Marco	1,791	2,332	1,541
TOTAL		9,149	12,690	17,295

[a]February-March; ground count.
[b]January; count from photographs.

INFLUENCES

Space

All the islands on which *A. australis* lives are also populated by *O. flavescens*. The competition with *O. flavescens* is reduced by several factors (Vaz-Ferreira and Sierra 1963), particularly the different breeding seasons of both species and their preference for different habitats. Steep, abrupt rock zones with crevices are preferred by *A. australis*, whereas flat areas are preferred by the sea lions (Vaz-Ferreira 1956).

The increase in fur seal populations has coincided with a decrease of the sea lion population, and part of the areas formerly occupied by sea lions is now occupied by fur seals. The population of *A. australis* is now probably near its original numbers since all areas formerly occupied by breeding fur seals appear to be recolonized.

Food

The coastal and oceanic areas off Uruguay are very rich in food, and there is no evidence that food may limit fur seal populations. Nevertheless the period of winter attendance on the higher parts of the islands has been reduced over the last few years. This suggests that the fur seals remain at sea longer than in previous years, at a time which coincides with the increase of populations and of fishing activities.

Competitors

Competition between fur seals and sea lions is reduced by the fact that the sea lion feeds in inshore waters and the fur seal goes farther out to deeper areas. Competition between fur seals and man is much less marked compared with sea lions, because the latter mainly follow fishing boats and feed more often on fishes caught in nets than do fur seals.

Predation

Apart from man, the known predators in Uruguay are several species of sharks which catch pups and attack adult females, and killer whales, *Orcinus orca*, which are sometimes seen near the islands during the breeding season.

Survival

Counts of dead pups in different parts of a rookery on Isla de Lobos from November to February of 1956 gave pup mortality rates of 10% to 20% (Vaz-Ferreira unpubl. data). Much higher mortality rates, reaching 80% in the Torres Islands (Ximenez 1973) can occur at times of adverse weather. Near Cabo Polonio, for example, there are frequently big storms during December and January, where southerly winds raise the sea level by 2 m. Many pups are swept away and are either drowned or driven ashore on mainland beaches where, in the absence of their mothers, they starve (Ponce de Leon 1983a).

There are no data for post-weaning survival. A record exists of a male tagged as a pup and killed when it was 21 years old.

REPRODUCTIVE PARAMETERS

Estrus

Ponce de Leon (1983a) recorded December as the month in which the majority of females reach oestrus and noted that it occurs between the fifth and eighth day after parturition.

First pupping

Tagged known-age females first pupped at the age of 4 years, which means that they were impregnated when they were 3 years old. The finding of a few pregnant females of body length 1.06-1.18 suggests that impregnation might have occurred at 2 years of age.

Table 4—Pregnancy rates in female South American fur seals of different size classes.

Size class	Pregnant	Non-pregnant	Total
1.18 or less	4	7	11
1.19 - 1.31	25	0	25
1.32 - 1.36	4	0	4
TOTAL	33	7	40

No information is available about age-specific fecundity of adult females, but some data on pregnancy rates in relation to size are found in Table 4 (summarized from Vaz-Ferreira 1976a).

Territorial status in males

No data on the minimum age of breeding males are available. Vaz-Ferreira, Prigioni and Ponce de Leon (unpubl. data) record that the overall length and number of ridges in the canines (probably a direct measure of age) of three reproductively active males were 157 cm and 9-10 ridges, 160 cm and 9 ridges, and 173 cm and 8-9 ridges.

The males that go to hauling-out grounds have sizes equivalent to the ones in the breeding grounds, in which case many of them have fresh wounds, or are smaller than the ones on the breeding areas (117 and 5-6 ridges, 157 cm and 8 ridges, 162 cm and 9 ridges).

REPRODUCTIVE ECOLOGY

Timing of pupping

Births of *Arctocephalus australis* in the Uruguayan islands occur during November and December. In 1981 and 1982 at Isla de Labos, 80% of the pups were born during the last week of November and the first and second weeks of December (Ponce de Leon 1983a).

Density at peak breeding season

Dividing number of individuals by surface occupied in breeding areas during the breeding season in Isla de Lobos (December 1980), we recorded 12 individuals in 20 m^2 (0.6 m^{-2}); 9 in 15 m^2 (0.6 m^{-2}); 27 in 30 m^2 (0.9 m^{-2}), and 9 in 20 m^2 (0.45 m^{-2}). These records suggest some variation in density at the peak period of breeding.

Gregariousness

During the breeding season, territorial groups are established on the shoreline or in areas at distances up to 150 m from it. These places are provided with pools or rocks giving shade, which allow the seals to stay on hot days. At high temperatures, all the members of a breeding group either go to sea, protect themselves under rocks, or put part of their bodies into the water. The distances between territorial males may vary according to topography and situation: on the water front, the males are usually at distances of 2 to 6 m and 15 m behind the shoreline. The spacing may vary from 4 m to 10 m and more if the groups are isolated in pools or hills.

Degree of polygyny

No reliable data are available. Ratios of males to females vary between 1:1 and 1:13.

ATTENDANCE PATTERNS AND LACTATION

Attendance patterns of females

The attendance ashore of females is strongly influenced by weather conditions, temperature of rocks, and insolation (Vaz-Ferreira and Palerm 1961; Ponce de Leon 1983a). When the soil is hot, particularly if it is more than 36°C, almost all breeding females come ashore during the night and nurse their pups either at night or in the early morning; if the temperature is lower and the surf is heavy, the mothers remain on land longer or even stay the whole day nursing their pups.

Attendance patterns of males

Adult males have a maximum of attendance from November to January. Territorial males may defend territories for up to 60 days without going to sea.

Duration of lactation period

The pup suckles ashore for a period that varies between 8 and 12 months. Most pups are weaned during their eighth month and few continue suckling until they are 12 months old. During the first seven months, milk constitutes the only stomach content, and after the eighth month the stomach contents include either milk or milk with items such as sand, small stones, and shells of molluscs (Ponce de Leon 1983b).

Duration of trips to sea and visits ashore

No quantitative data are available.

GROWTH

Fetus development

According to Ponce de Leon (1983a,b), there is a high correlation between length (L) and weight (W) of the fetus during the intrauterine gestation. A total of 177 fetuses were sexed, measured and weighed during 1981 and 1982. The sex ratio was 51.4% male and 48.6% female, and the growth curve obtained was

$$W = 0.27087\ L^{2.33654} \text{ with } r^2 = 0.98730.$$

W-L correlation for female fetuses was

$$W = 0.27758\ L^{2.36208} \text{ with } r^2 = 0.98770$$

and for male fetuses:

$$W = 0.25038\ L^{2.36244} \text{ with } r^2 = 0.98722.$$

The W-L correlation for female fetuses was better than for male fetuses, and at the end of the gestation period the male fetus was

slightly bigger than that of the female. There was no correlation between the length or weight of pregnant females and the length or weight of their respective fetuses.

Pup development

Weights of four neonates (Vaz-Ferreira 1982) were between 3,350 and 5,450 g. Vaz-Ferreira et al. (unpubl. data) measured seven newborn pups (three females and four males) in Isla de Lobos on 5 December 1980 and found that overall lengths for males were 60-65 cm and for females 57.5-60 cm.

Ponce de Leon (unpubl. data) measured and weighed six neonates (two males and four females); male overall lengths were 56 cm and females 58-62 cm. Weights for males were 4,010-4,020 g and for females 5,000-5,200 g. When pups were 10 months old, the males measured between 89-95 cm and weighed 20,200-24,100 g; females measured 86-93 cm and weighed 16,300-21,800 g (Ponce de Leon 1983a).

Adult sizes

Maximum overall lengths recorded in Uruguay were 188.5 cm for males and 142.5 cm for females. Maximum weights recorded were 159 kg for males and 48.5 kg for females (Vaz-Ferreira 1982).

FOOD

Milk composition

During the main suckling period (November or December through October), milk is the only stomach content of the pups (Ponce de Leon 1983a). Milk from different females was sampled throughout the year, and analysis revealed substantial variation in its quantitative composition. The lipid content was minimum in December (28.3-32.3%), higher in April (35.3-48.8%), maximum in September (53.7-57.1%) and decreased in October (51.7%). Water content varied, being maximum in December (45.6-59.3%), lower in April (41.3-50.4%), minimum in September (29.0-32.3%), and starting to increase in October (38.7%). Protein content was constant throughout the year, varying between 8.1% and 12.45%.

Adult diet

The feeding of adults probably occurs offshore; some individuals are often seen 200 km off Isla de Lobos where they probably feed.

Adult individuals taken ashore usually have empty stomachs, but sometimes fish otoliths, snails, prawns, and cephalopod beaks may be found. Stomach contents of 13 specimens drowned in trammel nets studied by Brownell (Vaz-Ferreira 1982) included the following fish: *Engraulis anchoita*, *Trachurus lathami*, *Cynoscion striatus*, *Pneumatophorus japonicus*, *Peprilus* sp. In the stomach of nine specimens found dead on the coast of Rio Grande do Sul (South Brazil), Pinedo and Barros (1983) found shrimps (*Pleoticus muelleri* and *Artemesia longinaris*), otoliths (*Paralonchurus brasiliensis* and *Micropogonias furnieri*), and one specimen of *Sympterigia acuta*. Five species of gastropods were also found.

ACKNOWLEDGMENTS

We thank the following for financial assistance to attend the Symposium and Workshop in Cambridge: Scientific Committee for Antarctic Research, UNESCO and Plan de Ciencias del Mar - URU 82/009 - UNESCO-PNUD. Funds for field work and equipment in Uruguay during November and December 1983 and January 1984 were also provided by Plan de Ciencias del Mar - URU 82/009 - UNESCO-PNUD.

CITATIONS

BERING SEA TRIBUNAL OF ARBITRATION.
1895. Fur seal arbitration: Proceedings of the Tribunal of Arbitration, convened at Paris under the treaty between the United States and Great Britain, concluded at Washington, 28 February 1892, for determination of questions between the two governments concerning jurisdictional rights of the United States to the waters of Bering Sea. Wash., D.C., Government Printing Office 6:213-215.

PEREZ FONTANA, H.
1943. Informe sobre la industria lobera (ciento diez anos de explotacion de la industria lobera en nuestro pais. Montevideo, Servicio Oceanografico y de Pesca, 70 p.

PINEDO, M. C., and N. B. BARROS.
1983. Analises dos conteudos estomacais do leao marinho *Otaria flavescens* e do lobo marinho *Arctocephalus australis* na costa do Rio Grande do Sul, Brasil. *In* VIII Simp. Latinoam. Oceanografia, Montevideo, Uruguay, nov. 28-2 dic. 1983. Resumenes, p. 25.

PONCE de LEON, A.
1983a. Aspectos de la reproduccion, crecimiento intrauterino y desarrollo postnatal del lobo de dos pelos sudamericano *Arctocephalus australis* (Zimmermann, 1783) en islas de la Republica Oriental del Uruguay. Tesis Licenciatura en Oceanografia Biologica, Universidad de la Republica, Fac. Humanidades y Ciencias, 93 p.
1983b. Crecimiento intrauterino y postnatal del lobo de dos pelos sudamericano, *Arctocephalus australis* (Zimmermann, 1783), en islas de Uruguay. *In* VIII Simp. Latinoam. Oceanografia, Montevideo, Uruguay, nov. 28-2 dic. 1983. Resumenes, p. 22.

VAZ-FERREIRA, R.
1950. Observaciones sobre la Isla de Lobos. Rev. Fac. Hum. Cienc. Univ. Uruguay 5:145-76.
1956. Etologia terrestre de *Arctocephalus australis* (Zimmermann) (''lobo fino'') en las islas uruguayas. Trab. Islas Lobos, Serv. Oceanogr. Pesca 2:1-22.
1976a. *Arctocephalus australis* (Zimmermann) South American fur seal. ACMRR/MM/SC/49, 13 p. Sci. Consult. Mar. Mamm., Bergen, Norway.
1976b. *Arctocephalus australis* (Zimmermann) South American fur seal. Addendum. ACMRR/MM/SC49 Add. 1, 3 p. Sci. Consult. Mar. Mamm., Bergen, Norway.
1982. *Arctocephalus australis* Zimmermann, South American Fur Seal. Mammals in the Seas. FAO Fish. Ser. 4(5):497-508.

VAZ-FERREIRA, R., and E. PALERM.
1961. Efectos de los cambios meteorologicos sobre agrupaciones terrestres de Pinnipedios. Rev. Fac. Hum. Cienc. Univ. Uruguay 19:281-93.

VAZ-FERREIRA, R., and B. SIERRA.
1963. Tolerancia en grupos biespecificos de Pinnipedios. *In* Proc. XVI Int. Congr. Zool., Wash., D.C., 1:250 (Summary).

VAZ-FERREIRA, R., E. LESSA, F. ACHAVAL, and A. MELGAREJO.
1985. Recuento de cachorros de lobos marinos *Arctocephalus australis* y *Otaria flavescens*, Isla de Lobos, Uruguay, en febrero de 1981. Bol. Soc. Zool. Uruguay, Segunda Epoca, 2:32-35.

VERITAS [E. J. Devincenzi].
1895. Importancia de las Islas de Lobos. Necesidad de su administracion en forma por medio de licitacion publica. Montevideo, Imp. Dornaleche y Reyes, 15 p.

XIMENEZ, I.
1973. Nota preliminar sobre la repoblacion de *Arctocephalus australis* en la Isla Rasa. Trab. Congr. Latinoam. Zool. 1(5):281-288.

South American Fur Seal, *Arctocephalus Australis*, in Peru

PATRICIA MAJLUF
Large Animal Research Group
Department of Zoology
University of Cambridge
34A Storey's Way
Cambridge CB3 ODT, United Kingdom

HISTORY OF HARVESTING

Abundant archaeological records show that fur seals were exploited by the ancient Peruvians as far back as 2000 B.C. (Bonavia 1982), but little else is known about the status and exploitation of *Arctocephalus australis*, South American fur seal, in Peru before 1940, chiefly because of failure to distinguish between the species and the sympatric South American sea lion, *Otaria flavescens*.

Many authors mention the presence of enormous numbers of seals along the Peruvian coast around the beginning of this century, and commercial exploitation apparently took place indiscriminately until 1946. Between 1925 and 1946, 806,525 seal skins were exported from Peru, averaging 44,252 skins per year (Majluf and Trillmich 1981), but it is not known to which species of seal they belonged.

By 1943 only a few small groups of *A. australis* survived in isolated areas in southern Peru (Gamarra Dulanto 1943; Gonzales Zuniga 1944). In 1946, the hunting of both species of seals was prohibited between the months of January and April (Piazza 1969), but it was not until 1959 that sealing was totally banned (Grimwood 1969). At present, despite this legal protection, seal poaching is a very common practice and is persistently carried out by local fishermen.

POPULATION SIZE AND TRENDS

Censusing methods in Peru have unfortunately never been standardized. Numbers have been estimated mainly by using direct counts of animals ashore, but censuses commonly vary in time of year, time of day, and number of locations censused. Tabulations also involve errors in species and age category identification as well as disregard for thermoregulatory and disturbance-induced movements (Majluf and Trillmich 1981). Therefore, numbers obtained from censuses can only be taken as rough estimates.

Between 1951 and 1979, the population of *A. australis* in Peru increased from 40 (Piazza 1969) to 20,255 (Majluf and Trillmich 1981). This increase appears to have taken place in the three main colonies which have held up to 90% of the total population over the last 20 years: San Juan, Paracas, and San Fernando. During this period, all other colonies appear to have remained more or less stable (Fig. 1).

During the 1982-83 El Niño, high mortality of all year classes, a large decrease in numbers at San Juan and San Fernando, and an increase in the numbers of previously smaller colonies further south were observed (Table 1). Unfortunately, the extent to which mortality and migration influenced these changes in numbers cannot be determined.

INFLUENCES

Space

Abundant breeding space appears to be available for *A. australis* along the coast of Peru; however, as described above, at present most areas within its range remain unused. Poaching seems to be the cause of this limited distribution, as indicated by the fact that the three main rookeries are particularly protected (San Juan and Paracas are both national reserves, and San Fernando is a very isolated area). On these three sites, density varies widely with time of year, time of day, and several other environmental and behavioral factors, but the manner in which these changes in density affect the species' mortality is not known.

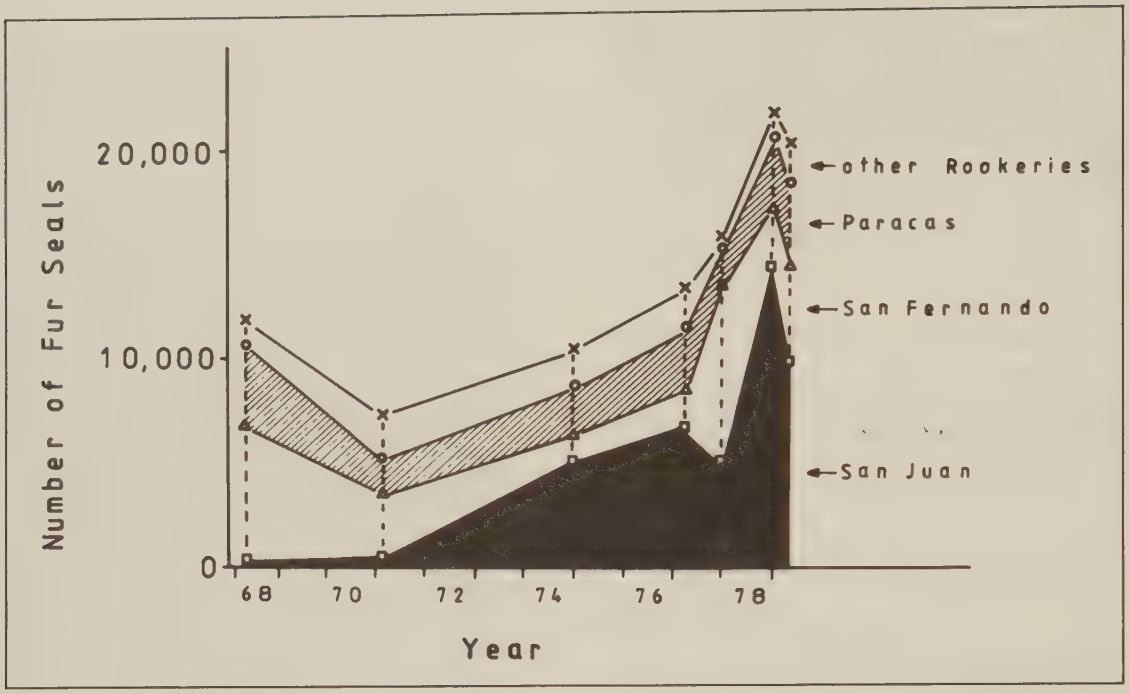


Figure 1—Contributions of the three largest colonies to the total population of fur seals in Peru (Majluf and Trillmich 1981).

Table 1—Numbers of fur seals at some colonies in southern Peru.

Colony	Lat. S	1979[a]	1983[b]	Observer[c]
Paracas	13°54′	4,246	—	—
San Fernando	15°08′	4,500	300	CH
San Juan	15°22′	9,644	2,000	PM
Cerro Pescadores	16°24′	—	4,000	CH
Hornillos	16°52′	805	600	CH
Morro Sama	18°00′	—	400	CH

[a]Data from Majluf and Trillmich 1981.
[b]Direct counts ashore taken around late April 1983.
[c]CH = Coppelia Hays, Dep. Zool., Univ. Fla., Gainesville, pers. commun.; PM = P. Majluf pers. observ.

Food

Within the past 15 years, the 1972 anchovy crash (Idyll 1973), continuous overfishing, and, lately, the 1982-83 El Niño, have presumably caused severe food shortages for *A. australis* in Peru. In "normal" El Niño years, starvation and mortality of young pups is to be expected, but under extreme conditions, like the 1982-83 event, juveniles and adults starve as well (pers. observ.).

Fish stocks in Peru have been extensively depleted, and under the present practices of overfishing, former abundance will probably never be reattained (Idyll 1973; Schaeffer 1970). Thus, even if total protection for *A. australis* were provided, it is unlikely to recover its former status in Peru.

Competitors

Fur seal rookeries are generally associated with the presence of sea lions and seabirds (e.g., Peruvian booby, *Sula variegata*; Guanay cormorant, *Phalacrocorax bougainvillei*; Peruvian pelican, *Pelecanus thagus*; and Humboldt penguin, *Spheniscus humboldtii*). All these are known to forage on the same pelagic fish species (anchoveta, *Engraulis ringens*; and sardine, *Sardinops sagax*), but the extent of competition among them is unknown. A detailed study of preferred fish sizes, foraging depth and ranges, and time of feeding for each species is still needed. In general, man's fishing activities appear to provide the main competition for fur seals in Peru.

Predation

Apart from man, fur seals appear to have no major predators in Peru. Occasionally, young sea lion males will feed on small fur seal pups ashore (pers. observ.) and, very rarely, sharks will attack adults feeding offshore (M. Rojo, guard at Punta San Juan, Peru, pers. commun.); however, information about the mortality rate of the seals is unavailable.

Reproductive parameters and reproductive ecology

The South American fur seal breeds between mid-October and mid-December in Peru, most births taking place in November (pers. observ.). By late November 1979, female density ranged between 0.6 and 1.0 females per m^2, and varied with temperature, time of day, and tide level. Overall group density varied between 0.5-0.7 animals per m^2 in the early morning and 1.3-1.5 animals per m^2 at noon, as animals moved back and forth between the dry areas and the tideline for thermoregulation (Trillmich and Majluf 1981).

Attendance patterns of females were studied between January and August 1983, outside the breeding season and under El Niño conditions. During this period, mean duration of foraging trips observed was 5.53 days (N=60, range 1-12 days; see Fig. 2a). There is no information on the duration of foraging trips in non-El Niño seasons. However, the emaciated state of pups suggests that either the foraging trips were longer than normal or that the mothers were not transferring as much milk to their offspring as in normal seasons (Trillmich et al. 1986).

Foraging trip length varied widely, but there was no correlation with changes in sea surface temperature, although the small sample

sizes involved do not mean that this relationship should be neglected in future research.

Mean duration of female visits ashore during the El Niño season was 1.25 days (N=67, range 0.5-3.0 days; see Fig. 2b). This value is very similar to those obtained for other species of *Arctocephalus* (Gentry and Kooyman 1986), and therefore may not relate to prey availability at sea.

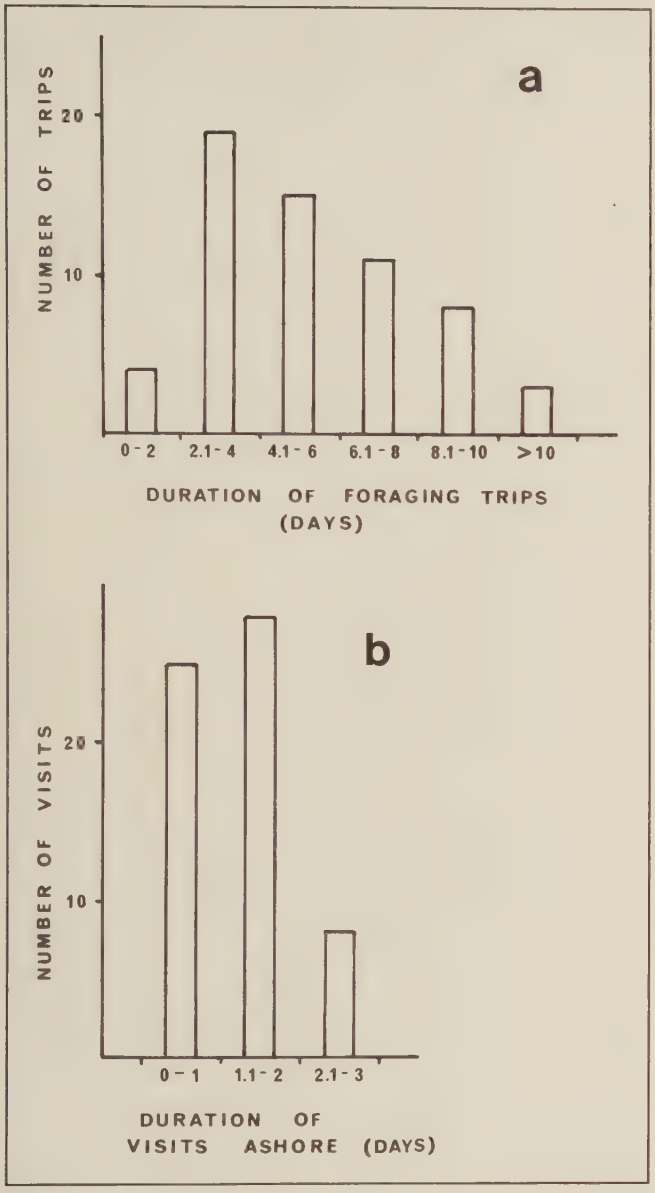


Figure 2—Duration of (a) foraging trips to sea (n = 60) and (b) visits ashore (n = 67), January-August 1983.

Table 2—Proportion (%) of females nursing offspring of different ages.

Categories	Feb. 1982 (normal) (n = 73)	Jan.-Aug. 1983 (El Niño) (n = 25)
Single pup of the year	56	62.6
Immatures (1-3 yrs old)	41.5	38.4
Two offspring simultaneously	2.5	—

Duration of lactation is still unknown, but apparently it very often exceeds 12 months (Trillmich and Majluf 1981). Counts of females nursing ashore (Table 2) indicate that a great proportion of females continue to nurse the offspring of the previous year, sometimes at the expense of the newly born pup.

Growth

No information is available on the growth rate of *A. australis* in Peru.

Food

Between January and August 1983, 100 scat samples were collected in Punta San Juan. Preliminary analysis of the otoliths indicates that *A. australis* in southern Peru forages mainly on *Sardinops sagax*, *Engraulis ringens*, and *Trachurus symmetricus*. Since these samples were collected during El Niño, a similar collection under normal environmental conditions is still needed.

ACKNOWLEDGMENTS

This work was funded by grants from Wildlife Conservation International (New York Zoological Society) and the Percy Sladen Memorial Fund to Patricia Majluf. It was also supported by the Max Planck Institut für Verhaltensphysiologie and by a grant of the National Geographic Society to G. L. Kooyman.

The Peruvian governmental organizations Pesca-Peru and Hierro-Peru kindly provided facilities and accomodation in San Juan. To all these, I am sincerely grateful.

CITATIONS

BONAVIA, D.
1982. Los gavilanes (precerámico peruano), mar, desierto y oasis en la historia del hombre. Ed. Ausonia, Lima, 512 p.

GAMMARRA DULANTO, L.
1943. Los lobos marinos. Bol. Comp. Admin. Guano XIX(4):121-131.

GENTRY, R. L., and G. L. KOOYMAN (editors).
1986. Fur seals: Maternal strategies on land and at sea. Princeton Univ. Press, 292 p.

GONZALES ZUNIGA, A.
1944. Lobos marinos, fuente de riqueza (del libro, Privilegios naturales del Peru). Bol. Comp. Admin. Guano XX(5):119-35.

GRIMWOOD, I. R.
1969. Notes on the distribution and status of some Peruvian mammals. Spec. Publ. 21, American Committee for International Wildlife Protection and N.Y. Zoological Society, 86 p.

IDYLL, C. P.
1973. The anchovy crisis. Sci. Am. 2287(6):22-29.

MAJLUF, P., and F. TRILLMICH.
1981. Distribution and abundance of sea lions (*Otaria byronia*) and fur seals (*Arctocephalus australis*) in Peru. Z. Saeugetierk. 46(6):384-393.

PIAZZA, A.
1969. Los lobos marinos en el Peru. Pesca y Caza 9:1-29.

SCHAEFFER, M. B.
1970. Men, birds and anchovies in the Peru current-dynamic interactions. Trans. Am. Fish. Soc. 99(3):461-467.

TRILLMICH, F., and P. MAJLUF.
1981. First observations on colony structure, behavior and vocal repertoire of the South American fur seal (*Arctocephalus australis*, Zimmermann, 1983) in Peru. Z. Saeugetierk. 46(5):310-322.

TRILLMICH, F., G. L. KOOYMAN, P. MAJLUF, and M. SANCHEZ-GRINAN.
1986. Attendance and diving behavior of the South American fur seal during "El Niño" in 1983. *In* R. L. Gentry and G. L. Kooyman (eds.), Fur seals: Maternal strategies on land and at sea. Princeton Univ. Press, 292 p.

Juan Fernández Fur Seal, *Arctocephalus philippii*

DANIEL TORRES N.
Subdireccion Cientifica
Instituto Antártico Chileno
Luis Thayer Ojeda 814, Correo 9
Santiago, Chile

INTRODUCTION

Since the rediscovery of *Arctocephalus philippii* in 1965 by Bahamonde (1966), attempts to begin detailed studies of this species have failed due to lack of financial and logistic support. Some research was carried out in 1970, 1975, and 1977-78, and was continued on a permanent basis from the 1982 to 1983 season.

Most of the publications about this species refer mainly to the results of opportunistic censuses (Aguayo 1971, 1976, 1979; Aguayo and Maturana 1970; Aguayo et al. 1971; Bahamonde 1966; Schurholz 1975; Schurholz and Mann 1977; Torres and Aguayo 1971; Torres et al. 1985) or to systematic studies (Repenning et al. 1971); historical reviews (Hubbs and Norris 1971); vocalizations (Norris and Watkins 1971); and parasites (Cattan et al. 1980). Various status summaries have been published (e.g., IUCN 1981), including recommendations about protection (Torres 1980).

HISTORY OF HARVESTING

Hunting of fur seals began a few years after Juan Fernández discovered the islands of San Felix and San Ambrosio (1554), the archipelago that bears his name. While there are no figures for the size of the population in those days, Hubbs and Norris (1971) quote observations made by the navigator William Dampier who visited Robinson Crusoe Island between 11 March and 8 April 1683. He wrote: "...Seals swarm as thick about this Island, as if they had no other place in the World to live in; for there is not a Bay nor Rock that one can get ashore on, but is full of them....Here are always thousands, I might say possibly millions of them, either sitting on the Bays, or going and coming in the Sea round the Island; which is covered with them (as they lie at the top of the Water playing and sunning themselves) for a Mile or two from the shore." Four years later (1687), Captain Davies of the ship *Bachelors Delight* left men salting skins at the island (King 1954). This was the beginning of large-scale exploitation of fur seals at Robinson Crusoe Island.

The navigator Philip Carteret visited Alejandro Selkirk Island between 1766 and 1769 and noted that "The seals were so numerous, that I verily think that if many thousands of them were killed in a night, they would not be missed in the morning..." (Bonner and Laws 1964).

Twenty-eight years later, hunting was at its peak there also. Hubbs and Norris (1971) and Pereira (1971) quote Captain Amasa Delano, who wrote: "When the Americans came to Más-á-Fuero, about the year 1797, and began to make a business of killing seals, there is no doubt but that there were 2,000,000 or 3,000,000 of them on the island. I have made an estimate of more than 3,000,000 that has been carried to Canton from thence in a space of 7 years. I have carried more than 100,000 myself, and have been at the place when there were the people of 14 ships or vessels at the island at one time killing seals." Sealing on this scale reduced numbers to the extent that Captain Morrel in 1824 noted that Más Afuera was an island "nearly without seals". Table 1 summarizes the principal details of exploitation between 1687 and 1898.

In recent years there has been some exploitation notably as a consequence of the erroneous interpretation of the ambiguous text of Decree No. 183 of 15 June 1976, that lifted the indefinite prohibition for the hunting of the Juan Fernández fur seal, replacing it by a "special prohibition". This meant that people could hunt as long as they had a permit from the administrative authority. That year the fishermen killed more than 300 animals. Now the law protects

the species totally and indefinitely. Nevertheless, owing to the critical economic situation of the fishermen, some of these animals have been killed in order to trade or sell in exchange for food.

Table 1—Historical information on fur seal hunting at the Juan Fernández Archipelago, San Felix and San Ambrosio Islands, from 1687 to 1898*.

Year	Hunter	Island	Number/Information
1687-90	Capt. Davies, ship *Bachelors Delight*	Más a Tierra	Left men saling skins on the island
1738	Pedro Le Guc	Más a Tierra	Hunting of seals with various gangs of Indian sealers
1791	Capt. S. Crowell, brigantine *Hancock*	Más Afuera	Hunted at Más Afuera
1792	Capt. J. Roberts, frigate *Jefferson*	San Felix and San Ambrosio	Obtained 13,000 skins
1792	Capt. W. R. Stewart, ship *Eliza*	Más Afuera	Took 38,000 skins
1794	Capt. J. Colnett, corvette *Rattler*	San Felix and San Ambrosio	Obtained salt at the Galapagos, for hunting at San Felix and San Ambrosio Islands
1797-1804	Fourteen ships from USA	Más Afuera	More than 3,000,000 skins were taken
1798	Capt. D. Greene, frigate *Neptune*	Más Afuera	15,000 skins; left a gang of seal hunters for 22 months
1798	Capt. D. Greene, frigate *Neptune*	San Ambrosio	35,000 skins
1798	Capt. E. Fanning, brigantine *Betsey*	Más Afuera	100,000 skins
1798	Capt. Liscomb, frigate *Maryland*	Más Afuera	20,000 skins
1798	Capt. G. Barney, frigate *Barclay*	Más Afuera	20,000 skins
1798	Vessels *Barclay Betsey* and *Neptune*	Más Afuera	60,000 skins
1800	Capt. W. Howell	Más Afuera	110,000 skins
1800	Capt. Green, frigate *Neptune*	Más Afuera	77,000 skins
1800	Capt. Folger, frigate *Minerva*	Más Afuera	23,000 skins
1800	Capt. U. Swain frigate *Mars*	Más a Tierra and Más Afuera	20,000 skins
1800	Capt. A. Delano	Más Afuera	More than 50,000 seals
1801	Sealer from USA	San Felix and San Ambrosio	A great number
1802	Capt. Briggs, frigate *Arctic*	Más Afuera	25,000 skins
1802	Capt. H. Fitch, frigate *Columbia*	Más Afuera	100,000 skins
1802	Capt. N. Storer, brigantine *Sally*	Más Afuera	Shipped 70,000 skins to Canton
1803	Capt. O. Fitch, whaler *Lady Adams*	Más Afuera	23,000 skins
1805	Capt. Moulthrop, frigate *Huron*	Más Afuera	19,000 skins
1807	Capt. C. Britnall, frigate *Triumph*	Más Afuera	50,000 skins
1807	Capt. Morrell	Más Afuera	Trade poor; took some animals
1824	Capt. Morrell	Más Afuera	Island nearly without seals
1891	Capt. Gaffney	Más Afuera	19 skins
1891-98	Settler Alfredo de Rodt	Más a Tierra	200-300 skins annually
1898	Foreign sealer	Más a Tierra	50 skins

*Data from Vicuna (1883), Albert (1901), Allen (1942), King (1954), Cabrera and Yepes (1940), Hubbs and Norris (1971) and Pereira (1971).

POPULATION SIZE AND TRENDS

Census methods

Censuses have been carried out from the shore and from fishing boats at sea. In the latter case binoculars were used. Large concentrations of seals were sometimes photographed and the resulting counts compared with the direct field count. Because seals are generally grouped in inaccessible places (rocks, caves, or small rocky beaches at the foot of cliffs) it is difficult to make accurate counts, and we estimate that at least 20% are overlooked.

Size

Based on the data in Table 1, it is likely that the total population of *A. philippii* towards the end of the 17th century exceeded 4 million animals. After such drastic overexploitation, the population's recovery must have been very slow, especially since there was still some hunting at a local level, carried out by Alfredo de Rodt who obtained the lease of the Juan Fernández Islands in 1877.

For nearly 100 years the species was considered to be extinct (King 1964). The first information to the contrary was provided by Bahamonde (1966) who observed and photographed about 200 animals at Alejandro Selkirk Island. In 1970 a complete census was carried out (Aguayo et al. 1971) which gave a minimum estimate of 750 animals. These and other data are summarized in Table 2. Only since the 1978-79 season has the census taken place in the middle of the reproductive period.

Table 2—Counts of *Arctocephalus philippii*[1].

Observer	Date	Island	No.	Census
N. Bahamonde	2 Dec. 65	Alejandro Selkirk	200	Partial
D. Bourne	27 Jan. 66	Santa Clara	8	Partial
K. Norris	2 Nov. 68	Robinson Crusoe	50	Partial
A. Aguayo R. Maturana	5 Mar. 69	Robinson Crusoe	192	Complete
A. Gonzalez	26 Mar. 69	Alejandro Selkirk	267	Complete
A. Aguayo	23 Feb. 70	Robinson Crusoe	246	Complete
D. Torres		Alejandro Selkirk	500	Complete
		Santa Clara	4	Complete
R. Gilmore D. Aguayo D. Torres	26 Jun. 70	San Ambrosio	2	Complete
G. Schurholz[2]				
G. Mann	1 Mar. 75	Alejandro Selkirk	130	Partial
H. de Rodt	15 Nov. 77	San Ambrosio	300	Partial
D. Torres	28 Oct. 78-	Alejandro Selkirk	1,820	Complete
P. Cattan	27 Jan. 79	Robinson Crusoe	512	Complete
J. Yanez		Santa Clara	84	Complete
D. Torres J. Cardenas G. Guerra	14 Nov. 82- 20 Dec. 82	Alejandro Selkirk	3,480	Complete
J. Cardenas	6 Dec. 83-	Alejandro Selkirk	4,544	Complete
G. Luna	3 Jan. 84	Robinson Crusoe	1,544	Complete
		Santa Clara	497	Complete

[1]From Torres et al. 1979 and updated.
[2]Schurholz and Mann (1977) estimated about 380-400 fur seals on Alejandro Selkirk Island in 1975.

Trends

The 6,300 animals censused in the 1983-84 season represent a mean annual increase of 16.5% since the census in the 1969-70 season and since the 1978-79 census, an increase of 21.4% per year. Under continuing protection, particularly from the attention of fishermen, the population should continue to increase substantially, since much suitable terrain remains to be colonized.

Influences

The historical data summarized by Hubbs and Norris (1971) suggest that nearly all the coastlines of the islands were full of animals. The survivors were presumably restricted to caves where they recolonized in places inaccessible to man.

The census of 1969 at Robinson Crusoe Island (Aguayo and Maturana 1970) established that there were only two main colonies with an average of 75 animals and four secondary colonies with an average of 10.5 animals. In 1983-84 there were seven main colonies averaging 115 animals and eleven secondary colonies averaging 17.8 animals.

At Alejandro Selkirk Island in 1979, there were only three colonies: the main one with 200 animals and two secondary ones with 12 and 35 animals, respectively. In 1983-84 there were 13 colonies of 51-1,003 individuals with an average of 332 animals.

Food

The original population, estimated in millions of animals, must have been sustained by substantial food resources, and it is unlikely that the present population is limited by food availability, although the original resources have been substantially depleted by commercial fisheries.

Competitors

In addition to fur seals, the early explorers reported enormous herds of southern elephant seals, *Mirounga leonina*, of which they gave precise descriptions and drawings as that published by Anson (1744). Elephant seals might have been important competitors for food and perhaps also for breeding space, but they are no longer found at Juan Fernández Archipelago, although they could return in the future (Torres 1981).

Subantarctic fur seals, *Arctocephalus tropicalis*, and Antarctic fur seals, *A. gazella*, are known only as vagrants at Juan Fernández Archipelago at present (Torres 1983a; Torres and Aguayo 1984). Small cetaceans, especially dolphins, *Tursiops* sp., are still abundant around San Felix and San Ambrosio islands (Aguayo 1975) and compete with the fur seals for fish and cephalopods. Other competitors for food include large populations of seabirds, especially gadfly petrels, *Pterodroma* spp., on Juan Fernández and the Desventuradas Islands. It is unlikely, however, that competitors for food with any of these will significantly retard the expansion of the fur seal population.

The development of the fishing activities at Juan Fernández and the Desventuradas Islands suggests that man is the most likely serious competitor. At present there is practically no control over catching fish and lobster, *Jasus frontalis*, and continued overexploitation could have adverse effects on the fur seal population. During the 1978-79 season when there was a scarcity of mackerels, *Trachurus symmetricus* and *Caranx longimanus*, the fishermen blamed the fur seal for the decrease of these fishes. Paradoxically, at present, with a larger fur seal population, the fishermen are not complaining of the scarcity of fishes.

Predation

Man is still the principal enemy of fur seals, and illegal hunting by fishermen could increase if their economic position deteriorates further. Information on natural enemies is based only on anecdotal observations or reports by fishermen. These indicate that sharks, *Prionace glauca* and possibly *Charcharodon*, attack seals, especially the young animals. Killer whales, *Orcinus orca*, and leopard seals, *Hydrurga leptonyx*, could also be potential predators; however, the latter is rarely seen at Robinson Crusoe Island (Torres and Aguayo 1971).

Survivorship

The only data available are for pup mortality, which was 8.2% at Alejandro Selkirk Island and 4.5% at Robinson Crusoe Island in 1983-84. In addition to the normal causes of death, some adults and pups appear to be afflicted with congenital blindness which is linked to abnormal pelage coloring. Nearly all juveniles or adults with this abnormality are males.

REPRODUCTION

Reproductive activity at the Juan Fernández Archipelago extends from the second week of November to the end of January. The peak of pupping occurs during the last week of November and first week of December.

In 1979 the average density of animals per hectare, excluding the harem zones, was 386 ± 157 with a maximum of 500 per hectare. An area of 36 m^2 per harem was calculated, with an average of four females per male (Torres et al. 1985). During the reproductive peak, the females form aggregations in which it is difficult to distinguish individuals of one harem from those of another. At such times females are separated by 30-40 cm.

GROWTH

The mean standard length and average weight of newborn pups at Alajandro Selkirk Island in November 1982 was as follows: males 68.2 cm and 6.9 kg ($n=130$); females 65.4 cm and 6.2 kg ($n=129$) (Torres 1983b). At about one month of age, in December 1983, the values were: males 71.8 cm and 7.3 kg ($n=84$), females 69.6 cm and 6.6 kg ($n=104$).

At Robinson Crusoe Island in January 1984, weights and measurements at about 2 months of age were: males 77.5 cm and 16.2 kg ($n=38$); females 75.2 cm and 10.0 kg ($n=44$). Standard lengths of adult males are about 2.10 m and of females about 1.50 m. Reliable weight data are unavailable.

FOOD

According to the fishermen, this fur seal feeds on various species of fish, squid, and lobsters. In the stomachs of animals that have died of natural causes, we have found only cephalopod beaks: *Dosidicus gigas*, *Octopotheuthis* sp., *Tremoctopus violaceus* (Torres unpubl. data), *Todarodes filippovae*, and *Moroteuthis banksii* (Castilla 1981).

CURRENT RESEARCH

In the 1982-83 season a program involving tagging pups and a regular population census was started. The use of immobilization techniques (Cardenas 1984) should enable additional data to be obtained from live animals. Most research will be directed toward acquiring behavioral and ecological information of relevance to the continued effective protection of this vulnerable species.

GENERAL RECOMMENDATIONS

During the 54th Meeting of the Survival Species Commission of the International Union for the Conservation of Nature and Its Natural Resources (IUCN), Torres (1980) made the following new proposals for a more effective protection of the Juan Fernández fur seal. These are still valid and, with certain modifications, urgently need implementation:

1. Maintain indefinitely the legal protection contained in the Supreme Decree No. 128, dated 29 May 1978.
2. Assure the permanence of the scientific investigations with the support of the national and regional authorities (e.g., Instituto Antártico Chileno and Corporacion Nacional Forestal).
3. Give information and previous basic training on conservation to authorities and officers (subordinates) who will perform their duties at the archipelago.
4. Instruct the personnel of the Armed Forces who may perform duties in any part of the range of the species.
5. Establish regular patrols with personnel of CONAF and Carabineros de Chile, when it is opportune, in the concentration and reproduction areas of the fur seals.
6. Maintain periodic inspections of ships and planes proceeding from the archipelago (and from San Felix and San Ambrosio) and establish a custom house at Robinson Crusoe Island.
7. Increase the number of game wardens (especially in Más Afuera Island) to keep guard on piers and airports of the archipelago.
8. Establish new ares of prohibited access, especially in those zones where new reproductive colonies have established.
9. Construct a small scientific base at Alejandro Selkirk Island.

If these recommendations were followed, the fur seal populations of the Juan Fernández Archipelago, San Felix and San Ambrosio Islands could reach a greater increase, becoming a potential resource. The advantage of having progressed in the study of its bio-ecology obviously assures the adequate future management of these populations.

ACKNOWLEDGMENTS

Thanks are due to John P. Croxall and Roger L. Gentry for their help and encouragement. Much of the data given here has been obtained in the field, thanks to the support provided by the World Wildlife Fund (WWF) and the International Union for the Conservation of Nature and Its Natural Resources (IUCN), through Project 1410 WWF/IUCN; the collaboration of the Corporacion Nacional Forestal (CONAF) and the Ministerio de Relaciones Exteriores, through the Instituto Antártico Chileno (INACH); and also the collaboration of the Chilean Embassies in Washington and Berne. I thank them all.

I am grateful to Miss Patricia Torres for typing the manuscript and to Mr. Raymond Peake for kindly translating it into English.

CITATIONS

AGUAYO, A.
1971. The present status of the Juan Fernández Fur Seal. K. Nor. Vidensk. Selsk. Skr. 1:1-4.
1975. Progress report on small cetaceans in Chile. J. Fish. Res. Board Can. 32:1123-1143.
1976. Juan Fernández Fur Seal. Documento presentado a la Reunion de Trabajo sobre Pinipedos (WP 44), Consulta Cientifica sobre los Mamiferos Marinos y su Medio (mimeo). Bergen, Noruega, 6 p.
1979. Juan Fernández Fur Seal. *In* Mammals in the seas. FAO Fish. Ser. 5(2):28-30.

AGUAYO, A., and R. MATURANA.
1970. Primer censo de lobos finos en el archipielago de Juan Fernández. Biol. Pesq. 4:3-15.

AGUAYO, A., R. MATURANA, and D. TORRES.
1971. El lobo fino de Juan Fernández. Rev. Biol. Mar. 14(3):135-149.

ALBERT, F.
1901. Los pinipedos de Chile. Imprenta, Litografia y Encuadernacion Barcelona. Santiago de Chile, 59 p.

ALLEN, G. M.
1942. Extinct and vanishing mammals of the western hemisphere with the marine species of all the oceans. Spec. Publ., Amer. Comm. Int. Wildl. Protect. 11:1-620.

ANSON, G.
1744. Voyage autour du monde (Journey around the world). Livre II, chapitre premier, p. 107-113. Publie par Richard Walter. Chez Henru-Albert Gosse, & Comp. Libraries & Imprimeurs A. Geneve.

BAHAMONDE, N.
1966. El mar y sus recursos. *In* Geografia economica de Chile, Primer apendice, p. 81-85. CORFO, Santiago, Chile.

BONNER, W. N., and R. M. LAWS.
1964. Seals and sealing. *In* Priestly, R., R. J. Adie, and G. Q. Robin (eds.), Antarctic research. A review of British scientific achievement in Antarctic, p. 163-198.

CABRERA, A., and J. YEPES.
1940. Mamiferos Sudamericanos. Compania Argentina de Editores, Buenos Aires, 370 p.

CARDENAS, C.
1984. Evaluacion de un metodo de inmovilizacion quimica a distancia en pinipedos otaridos en condiciones naturales. Tesis Med. Vet. y Lic. Cs. Pecuaria, Fac. Cs. Agrarias, Veterinarias y Forestales, U. de Chile, 119 p.

CASTILLA, J. C.
1981. Informe de actividades del Taller Cientifico sobre identificacion de mandibulas de cefalopodos (Plymouth, 1981). Bol. Antárt. Chil. 1(1):23-25.

CATTAN, P., J. YANEZ, and D. TORRES.
1980. Helmintos parasitos del lobo fino *Arctocephalus philippii* (Peters, 1866) de Juan Fernandez. Bol. Chil. Parasitol. 35:73-75.

HUBBS, C. L., and K. S. NORRIS.
1971. Original teeming abundance, supposed extinction, and survival of the Juan Fernández fur seal. Antarct. Res. Ser. 18:35-52.

IUCN. International Union for the Conservation of Nature and Its Natural Resources.
1981. Juan Fernández Fur Seal, *Arctocephalus philippi* (Peters, 1866). Vulnerable. Order Pinnipedia, Family Otariidae. RDB p. 403-405.

KING, J. E.
1954. The Otariid seals of the Pacific Coast of America. Bull. Br. Mus. (Nat. Hist.) 2(10):311-337.
1964. Seals of the world. Br. Mus. (Nat. Hist.), 154 p.

NORRIS, K. S., and W. A. WATKINS.
1971. Underwater sounds of *Arctocephalus philippii*, the Juan Fernández fur seal. Antarct. Res. Ser. 18:169-171.

PEREIRA, S. E.
1971. Los primeros contactos entre Chile y los Estados Unidos (1779-1809). Historia de las Relaciones Internacionales de Chile, Editorial Andres Bello, Santiago-Chile. 353 p.

REPENNING, C. A., R. S. PETERSON, and C. L. HUBBS.
1971. Contributions to the systematics of the southern fur seals, with particular reference to the Juan Fernández and Guadalupe Species. Antarct. Res. Ser. 18:1-34.

SCHURHOLZ, G.
1975. Technical Reports on duty travel to Más Afuera as related to the Goat-Seal project, 8 February-23 March 1975. FAO Memo, 15 p. (Unpubl.).

SCHURHOLZ, G., and G. MANN.
1977. Comments on the populations of the Juan Fernández fur seal (*Arctocephalus phillippii*). Int. Game Biol. Conf., Atlanta, 16 p.

TORRES, D.

1980. Proposiciones para la proteccion del lobo fino de Juan Fernández, *Arctocephalus philippii* (Peters, 1866) y de su medio. (Pinnipedia: Otariidae). 54th Meeting of the Survival Service Commission, IUCN, 1-4 October 1980. Univ. Florida, Gainesville, 18 p.

1981. Notas sobre el elefante marino del sur, *Mirounga leonina* (Linn. 1758) y hallazgo de un ejemplar en Chanaral, III Region, Chile (Pinnipedia: Phocidae). Bol. Antárt. Chil. 1(2):10-14.

1983a. Reuniones sobre pinipedos realizadas en Pretoria por el Grupo de Expertos de SCAR. Bol. Antárt. Chil. 3(2):41-43.

1983b. Slow recovery of the Juan Fernández Fur Seal population. Field narrative report of the Juan Fernández Fur Seal Project 1410 WWF/IUCN. 1st. Stage, Nov.-Dec. 1982, 63 p.

TORRES, D., and A. AGUAYO.

1971. Algunas observaciones sobre la fauna del archipielago de Juan Fernández. Bol. Univ. Chile 2(212):26-37.

1984. Presence of *Arctocephalus tropicalis* (Gray 1872) at the Juan Fernández Archipelago, Chile. Acta. Zool. Fenn. 172:133-134.

TORRES, D., J. YANEZ, and P. E. CATTAN.

1979. Mamiferos marinos de Chile: Antecedentes y situacion actual. Biol. Pesq. 11:49-81.

TORRES, D., P. E. CATTAN, and J. YANEZ.

1985. First census of the Juan Fernández fur seal *Arctocephalus phillippii* (Peters) during the breeding season, 1978-1979. Natl. Geogr. Soc. Res. Rep. 18:733-743.

VICUNA, M. B.

1883. Juan Fernández. Historia verdadera de la isla Robinson Crusoe. (R. Jover, ed.). Santiago, Chile, 834 p.

Guadalupe Fur Seal, *Arctocephalus townsendi*

LUIS A. FLEISCHER
Centro Regional de Investigacion Pesquera
Km. 1 Carretera a Pichilingue
La Paz, Baja California Sur
Mexico

INTRODUCTION

The Guadalupe Fur Seal, *Arctocephalus townsendi*, is the only member of the genus *Arctocephalus* which is found north of the Equator. This account describes the major features of the population biology of the species, synthesizing the results of research carried out during the breeding seasons of 1975, 1976, and 1977 in Guadalupe Island, at the only breeding place of the species. This account relies heavily on the population data recorded by Fleischer (1978); behavioral aspects of the species are described by Pierson (1987).

HISTORY OF HARVESTING

As for other fur seal species, there is a scarcity of information on the abundance of the *A. townsendi* population prior to and during the large-scale commercial sealing. However, dates engraved on the remaining stone walls of the sealing station ruins on Guadalupe Island indicate at least nine visits to Guadalupe by sealers between 1834 and 1881, by which time this population, as well as other marine mammal populations, was commercially depleted and was almost biologically extinguished.

There are also records of early sealing during the initial settling of California by North Americans (Scammon 1874; Allen 1899; Townsend 1899), which suggest that exploitation of the species may have started on islands off Baja California, Mexico, just before the end of the 18th century. The fur seals inhabiting the rookeries of Guadalupe Island were slaughtered during the early 19th century, principally in the first two decades (Townsend 1899; Hubbs 1956a,b), and the last reported catch was in 1894, by which time the population had nearly been exterminated (Hubbs 1956b).

Table 1 summarizes the available published records of fur seals taken on Guadalupe and San Benito Islands from 1834 to 1894 (Townsend 1899; Hubbs 1956a) which permit a reconstruction of the exploitation. According to these reports, the total number of fur seals killed during this 60-year period was 6,644. Because of the competitive trade and secrecy of the sealers, however, there is not a complete data set of the captures and it is only possible to average the yearly captures from 1877 to 1894, yielding a value of 365 fur seals for those islands only.

Hubbs (1956a) proposed an estimate of the original population of Guadalupe Island of at least 200,000 fur seals. However, based on the available information, Fleischer (1978) proposed a much lower estimate of only 20,000. At present, the Guadalupe fur seal is completely protected by Mexican laws, and in 1975 Guadalupe Island was declared a sanctuary for pinnipeds by the Mexican government because of the presence of the fur seals and two other sympatric pinnipeds, the northern elephant seal (*Mirounga angustirostris*) and the California sea lion (*Zalophus californianus*).

POPULATION SIZE AND TRENDS

As shown in Table 2, the largest number ever recorded in the recent history of *A. townsendi* was 1,073 fur seals counted in 1977. This figure is based on direct counts made at breeding time on the east side of the island, the only portion which they inhabit at present. For this survey direct counting methods were used, which were adequate for a small population like *A. townsendi*.

Furthermore, the data produced by the three different types of surveys (simultaneously counting by vessel, by small boat [outboard

Table 1—Available records of fur seals taken on Guadalupe and San Benito Islands, 1834-1894 (Townsend 1899; Hubbs 1956a) (from Fleischer 1978).

Year	Expedition	Island	Fur seals taken	Notes
1834				
1835		Guadalupe		No data exist but dates are chiseled into the walls of the ruins in Guadalupe Island.
1837		Guadalupe		
1839		Guadalupe		
1849		Guadalupe		
1851	W. E. Bryant	Guadalupe		
1866-winter		Guadalupe		
1869		Guadalupe		
1871				
1876-1877	George W. Chase	San Benito	"Few"	Report is incomplete but mentioned presence of pups.
1877	Capt. Charles Haritwen	Guadalupe	800	Reported take by several boats.
1877	Capt. Kathgard	Guadalupe	15 1,000	Kathgard reported 15 taken and 1,000 taken by other boats.
1879	James Borges and Fred Sinnon	Guadalupe and San Benito	1,550	They worked in both places.
1880	Other boats reported by	Guadalupe	500	Reported pups being born in the middle of June. Also big concentrations of fur seals in the rookeries of the west side, about 600-700 seals together.
May 1-20	Capt. Charles Haritwen	San Benito (east)	2	
May 24		Guadalupe		
1880	George W. Chase	Guadalupe		Reported about 3,000-4,000 seals alive and breeding in June-July. Also reported sightings of the fur seals 100 mi west of Guadalupe. Chase noted the presence of fur seals all year around.
June			185	
July-August			150	
September			75	
1881		Guadalupe		No data exist but date is chiseled into the walls of the ruins of Guadalupe Island.
1883-1884	Capt. G. E. Wentworth	Guadalupe	2,000	Reported 4,000 fur seals alive. Wentworth took half and other boats broke up the rookery.
1884	C. H. Townsend	Guadalupe	0	No fur seals reported due to bad weather.
1885	James M. Niles	Guadalupe	200	Niles made six trips to Guadalupe, reported 2,000 fur seals alive with many pups.
1885	Capt. Flupp	Guadalupe	1	Saw only five alive.
1889-February	C. H. Townsend	Guadalupe	0	Reported three harbor seals.
1890	George M. Hunt	Guadalupe	0	Saw only four alive.
1891-June	Burke and Farwell	San Benito	4	Statement by Hunt.
1891-December	George M. Hunt	Guadalupe	5, 1 pup	Only seven pups were seen.
1891-1892	Capt. F. M. Gaffney	Guadalupe	0	Reported no seals left.
1892	C. H. Townsend	Guadalupe	1	One killed but not secured. Seven were reported about 1 mi from the island. Townsend collected four skulls on west side of island.
May 16-25				
1893	A. W. Anthony	Guadalupe	36	
1894	A. W. Anthony	Guadalupe	15	

engines], and by walking on the shore), provided a way to correct the values of other routine counts and to derive a correction factor applicable for future censuses. The method is based on an Inverse Prediction Technique, which is fully discussed in Fleischer (1978). The highest recent count of this species is presented by age and sex in Table 3. The different results obtained by the use of different census methods indicated a significant error in the numbers obtained by boat and vessel surveys. These counts yielded only half of the total numbers of animals observed on foot surveys and thus extremely biased results for the number of pups present at the study areas.

This table can also be used to analyze the composition of stock of the Guadalupe fur seal herd, which is compared with the data collected in 1976, when only a portion of the entire breeding range was successfully censused (Table 4). The herd composition was similar in both 1976 and 1977; mature females formed the largest component in both seasons and the female/male ratio was also similar. Estimated pup production was 0.50 and 0.58 pups per female over the entire colony in 1976 and 1977, respectively, and 0.62 and 0.65 pups per male for those years.

The data in Table 2 suggest that Guadalupe fur seal numbers are increasing (Fleischer 1978); however, this might only reflect a redistribution of the existing population. Furthermore, census information available prior to 1977 is not fully comparable because of the different census methods used by other researchers.

At present, the stock is scattered along the east side of the island (Fig. 1) where a small amount of expansion and colonization has taken place. The species may also be recolonizing parts of its historical range (Fig. 2), especially at San Miguel Island (R. DeLong, Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115, pers. commun.) and San Nicolas Island (Stewart et al. 1987). The scattered stock on Guadalupe Island includes a high concentration of mature animals near the place called Nursery and a concentration of juvenile fur seals near Lobster Camp (Fig. 1). Considering historical information on the fur seal distribution on the island and the seal's preference for a rocky habitat, space

Table 2—Census (all sources) of Guadalupe fur seal, 1954-77 (from Fleischer 1978).

Field party or observers	Date	Total
C. Hubbs, W. Sefton, E. Arebalo	November 1954	14[a]
C. Hubbs, V. Scheffer	June 1955	30-35
R. Gilmore	December 1955	70-75
R. Gilmore	June 1956	92
C. Hubbs, G. Ewing, J. Berdegue	August 1956	30
C. Hubbs et al.	August 1956	71-76
J. Berdegue	February 12, 1957	107
C. Hubbs et al.	October 24-31, 1957	134
D. B. Lluch, M. Pilson	February 1964	240
D. B. Lluch, M. Pilson, L. Irving	November 1964	252
D. Rice, W. Kenyon, D. Lluch	January 1965	285
D. Rice, W. Kenyon, D. Lluch	March 1965	211
C. Hubbs	April 1966	372
R. Peterson et al.	May 1967	198
R. DeLong	October 1967	149
R. Brownell et al.	April 1968	148
R. Brownell, R. DeLong, R. Schreiber	June 1968	314
L. Fleischer, M. Pierson	December 1971	[b]
R. S. Paterson	January 1975	254
M. Pierson, C. Cox, L. Fleischer	June-July 1975	80
L. Fleischer, D. Margetts	June-July 1976	355
M. Pierson, B. LeBoeuf et al.	February 1977	470
L. Fleischer, M. Pierson, M. Riedman	June-July 1977	1073

[a]Rediscovered the Guadalupe fur seal.
[b]This trip saw only a few females and pups.

Table 3—Total counts of various types of surveys of Guadalupe fur seals *Arctocephalus townsendi*, 1977 (from Fleischer 1978).

Type of survey	Adult		Sub-adults	Juveniles	Pups	In the water plus undetermined	Total
	Male	Female					
Maximum count (all surveys combined)	326	412	23	70	204	38	1,073
Maximum count foot	305	382	22	79	205	39	1,032
Maximum count small boat (AVON)	254	215	6	44	11	61	591
Maximum count sailboat circumnavigation	279	163	40	31	27	6	546
Maximum count sailboat by areas	257	197	8	26	13	35	536

Table 4—Stock composition of Guadalupe fur seal *Arctocephalus townsendi* based on censuses of 1976-77 (modified from Fleischer 1978).

	Percent	
	1976	1977
Mature males	25	30
Mature females	28	38
Pups	16	19
Juveniles	4	7
Subadults	20	2
Unidentified plus in the water	6	4
TOTALS	355	1,073
Ratios:		
Females/males	1.12	1.26
pups/females	0.85	0.50
pups/males	0.65	0.62

is not a major factor affecting overall population growth, contrasting significantly with the two other sympatric pinnipeds on the island.

The marine habitat of this fur seal is favored by upwellings (Hubbs 1948, 1960) which presumably provide sustained food resources. Although there is no information on the food preferences of this species, it is unlikely that food availability or competition with other marine mammals in the area is limiting population growth.

There are no land predators of the fur seals at Guadalupe, but there are major predators around the area, such as the great white shark (*Carcharodon carcharias*). Cyclonic storms also seem to be a source of significant pup mortality, but no pup mortality estimates have been made.

REPRODUCTIVE PARAMETERS

Because of the species rarity and the need to avoid disturbance to breeding colonies, there is only anecdotal information available. Discovery of a dead female in 1976 which measured 137.67 cm and had a living non-molted pup at her side, was indication that she at least was a sexually mature animal. The carcass was too decomposed for examination of the ovaries.

A naturally marked male animal (lacking a left hind flipper) was photographed for the first time in 1968 breeding in a cave on the east side of the island, and subsequently reidentified at the same location in 1975 and 1976. This suggests that it was reproductively active for at least 9 years and indicates a strong site fidelity.

REPRODUCTIVE ECOLOGY

Pupping occurs in the summer from 15 June reaching a peak around 21 June. The last pups born were seen on 22 July 1976 and 17 July 1977 (Fleischer 1978).

Mature bulls showed much aggression, and several males were observed with scars and severe body injuries as a result of territorial fights. Males exhibited sexual interest in females from mid-June until we left the island in late July. Two copulations were observed; one in 1976 lasted 15 minutes and one in 1977 only 5 minutes. In the central part of their breeding range, the spacing of territories averaged 19.8 m apart.

GROWTH AND FOOD

No information is available on growth rates of *A. townsendi* pups. Table 5 presents measurements and estimated weights of available Guadalupe fur seal specimens.

Nothing is known of the diet of *A. townsendi*. It is assumed to prey on different types of fish, and a squid beak was reported in a vomit (M. O. Pierson, Inst. Mar. Stud., Univ. Calif., Santa Cruz, CA 95064, pers. commun.).

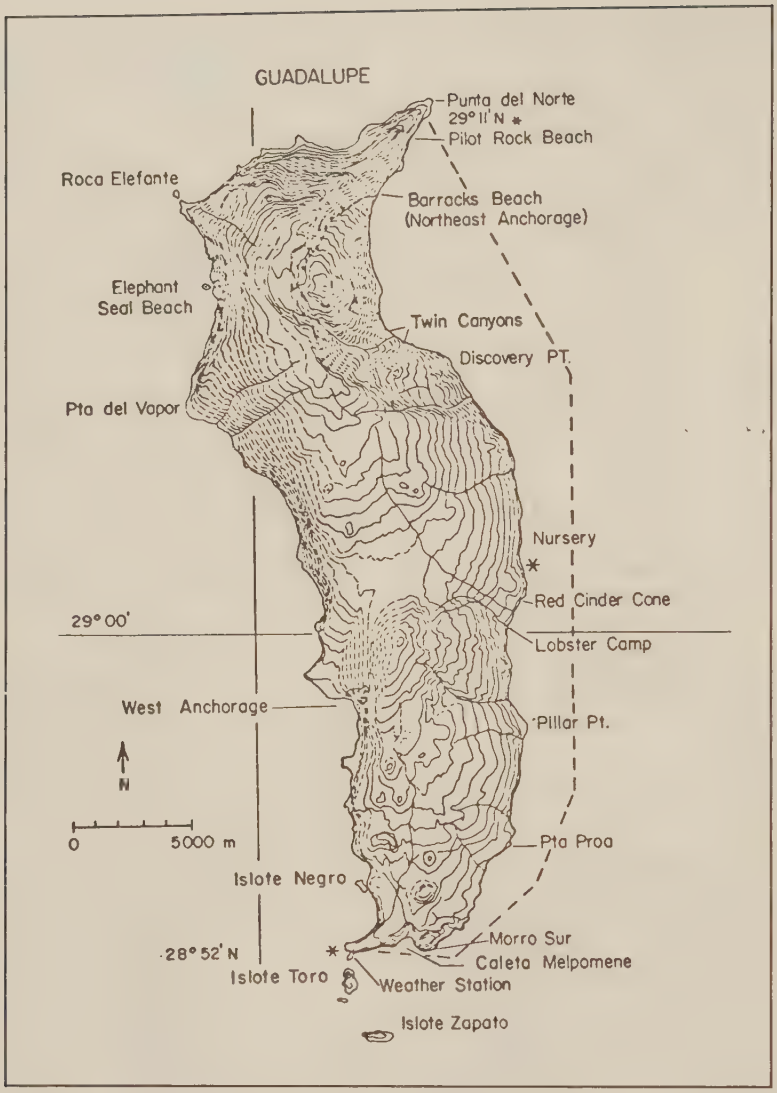


Figure 1—Present distribution of Guadalupe Fur Seal breeding population (Summer 1977). Dotted line indicates area occupied by *Arctocephalus townsendi* (from Fleischer 1978).

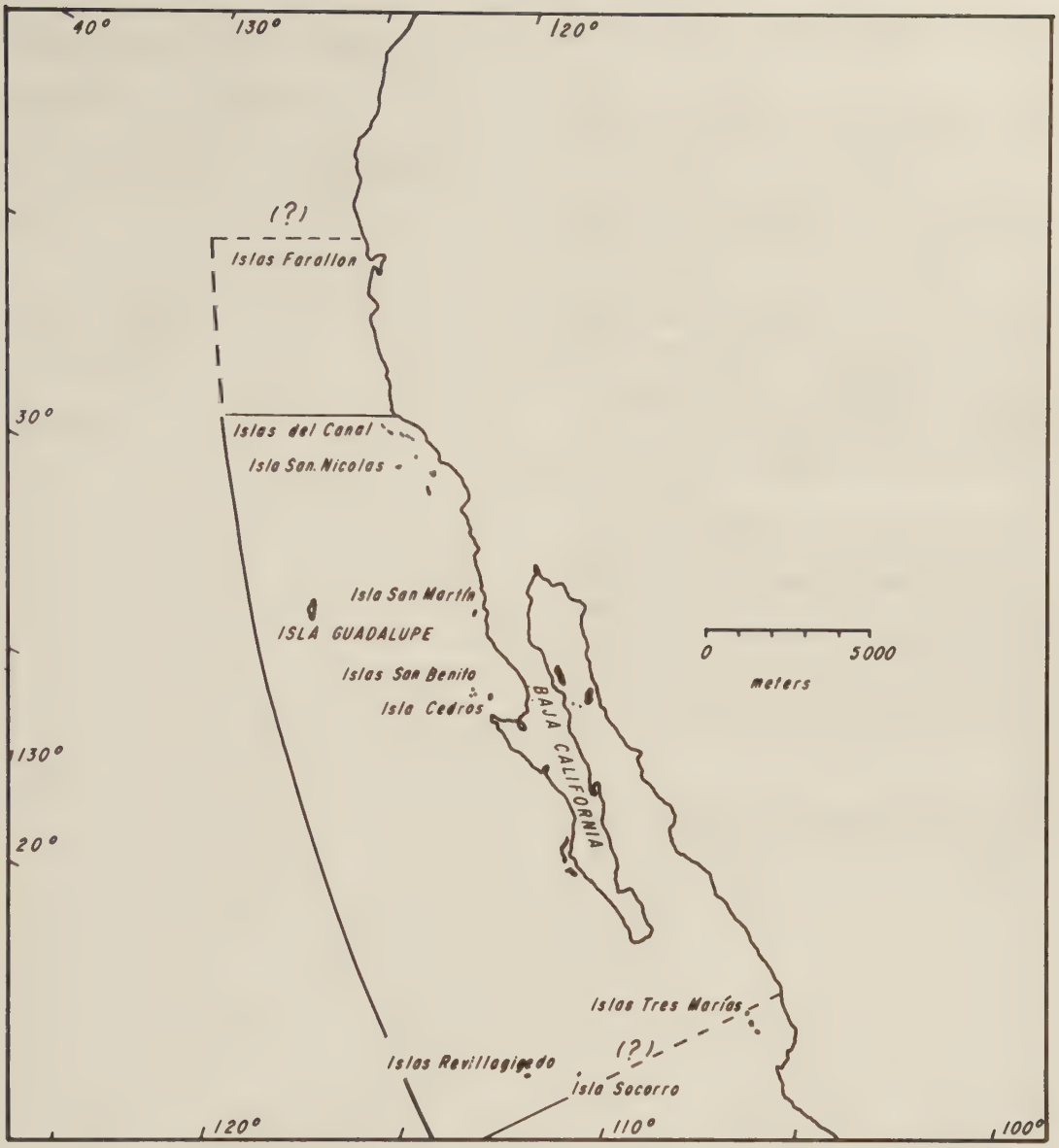


Figure 2—Historic range of *Arctocephalus townsendi* (from Fleischer 1978).

Table 5—Measurements of the Guadalupe fur seals taken in 1976-77 (from Fleischer 1978).

Measurements	Male adult[a] 1977	Female[b] 1976	Newborn pup (nonmolted) 1976
Standard length (cm)	193.04	137.16	—
Curvilinear length (cm)	196.85	—	57.15
Anterior length front flipper (cm)	58.42	34.29	21.59
Anterior length hind flipper (cm)	39.37	26.67	16.51
Axillary girth (cm)	125.73	—	—
Thickness of blubber (cm)	3.81	not present	—
Estimated weight (kg)	160-170	45-55	—

[a]Measurements were taken during the autopsy of the dead specimens found on 24 June 1977 and 19 July 1976.

[b]Measurements were taken from a live female (orphan) pup found on 19 July 1976.

CITATIONS

ALLEN, J. A.

1899. Fur seal hunting in the southern hemisphere. *In* Jordan, D. S., The fur seals and fur seal islands of the North Pacific Ocean, p. 307-319. Doc. 2017, 3(12) U.S. Gov. Print. Off., Wash., D.C.

FLEISCHER, L.

1978. The distribution, abundance, and population characteristics of the Guadalupe fur seal *Arctocephalus townsendi* (Merriam 1897). M.S. Thesis, Coll. Fish., Univ. Wash., Seattle, 93 p.

HUBBS, C. L.

1948. The zoological evidence: Correlation between fish distribution and hydrographic history in the desert basins of western United States. The Great basins, with emphasis on glacial and postglacial times. Bull. Univ. Utah 38(20): 17-166.

1956a. Back from oblivion. Guadalupe Fur Seal: still a living species. Pac. Discovery 9:14-21.

1956b. The Guadalupe Fur Seal still lives. Zoonoses 29:6-9.

1960. The marine vertebrates of the outer coast, Pt. 2. Marine biotas. Syst. Zool. 9(3-4):114-137.

PIERSON, M. O.

1987. Breeding behavior of the Guadalupe fur seal, *Arctocephalus townsendi*. *In* Croxall, J. P., and R. L. Gentry (eds.), Status, biology, and ecology of fur seals, p. 83-94. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 51.

SCAMMON, C. M.

1874. The marine mammals of the northwestern coast of North America. John H. Carmany Co., San Franc., 319 p.

STEWART, B. S., P. K. YOCHEM, R. L. DeLONG, and G. A. ANTONELIS, Jr.

1987. Interactions between Guadalupe fur seals and California sea lions at San Nicolas and San Miguel Islands, California. *In* Croxall, J. P., and R. L. Gentry (eds.), Status, biology, and ecology of fur seals, p. 103-106. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 51.

TOWNSEND, C. H.

1899. Pelagic sealing. With notes on the Fur Seals of Guadalupe, The Guadalupe, the Galapagos, and Lobos Islands. *In* The fur seals and fur seals islands of the North Pacific Ocean, p. 233-274. U.S. Gov. Print. Off., Wash., D.C.

New Zealand Fur Seal, *Arctocephalus forsteri*, within the New Zealand Region

ROBERT H. MATTLIN
Fisheries Research Division
P.O. Box 297
Wellington, New Zealand

HISTORY OF HARVESTING

Fur seals, *Arctocephalus forsteri*, were first taken commercially in New Zealand in 1792-93, when a gang working out of Dusky Sound, Fiordland, took 4,500 skins (McNab 1907). Sealing in the New Zealand region (including New Zealand, Stewart Island, Chatham Islands, and the New Zealand subantarctic islands: Antipodes, Auckland, Bounty, Campbell, Macquarie, and Snares Islands) did not begin in earnest until 1803, following the decline of the Australian Bass Strait seal fishery. The New Zealand seal fishery then expanded rapidly with the discovery of the Foveaux Strait sealing grounds and the New Zealand subantarctic islands with their extensive fur seal colonies (Fig. 1). Harvesting was indiscriminate and the resident fur seal populations were soon depleted. The New Zealand seal fishery was nearly over by 1812; few sealers were working the New Zealand region after 1830 (Wilson 1974a).

The sealing trade was very competitive and, as a result, shrouded in secrecy. Figures for skins taken and the recorded localities from which they were collected are often inaccurate, misleading, or nonexistent. However, available records indicate that hundreds of thousands of skins were taken from the region. It was not unusual for individual gangs to return with 15,000 or more. One gang alone took 60,000 skins from the Antipodes Islands in 1804-05, and during one season prior to 1815, over 100,000 were reported taken

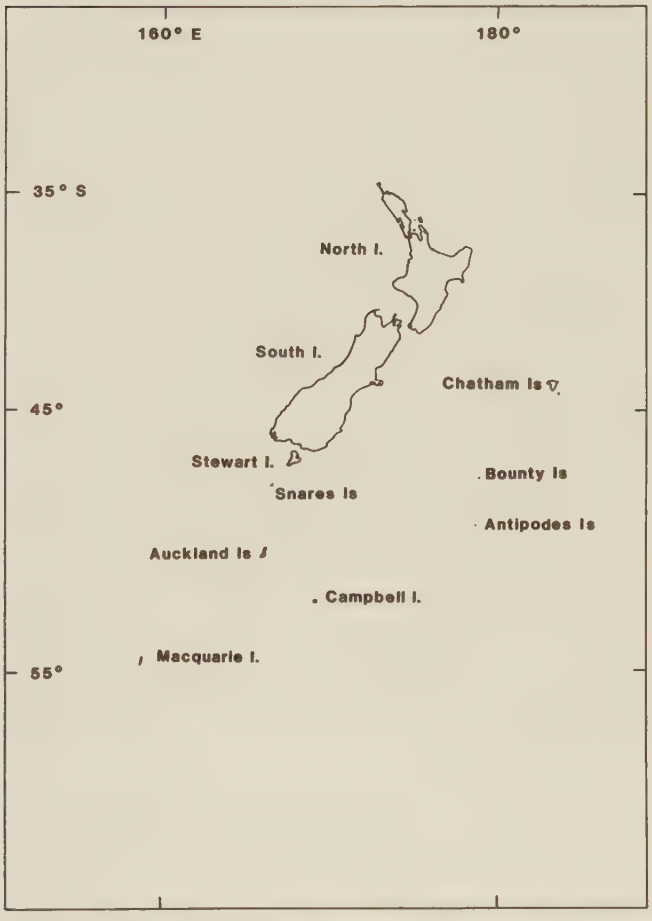


Figure 1—Islands within the New Zealand region where New Zealand fur seals bred historically, or are found now.

from Macquarie Island (McNab 1907). Fur seal populations could not sustain such intense harvesting pressure and soon collapsed. Fur seals were exterminated at the Antipodes Islands and nearly so at the Bounty Islands (Sorensen 1969b; Taylor 1982). None were seen at Macquarie Island during a visit by Captain Bellinghausen in 1820 (McNab 1907), and Captain Morrell of the *Antarctic* reported no fur seals at either the Auckland or Snares Islands in January 1830 (Morrell 1832).

The fur seal fishery was officially closed by the New Zealand Government in 1894. Restricted licenses were issued between 1913 and 1916, and again in 1922-24 for Campbell Island only. The number of fur seals taken during the former season is unknown, but 350 of a permitted 400 were taken from Campbell Island during the latter (Sorensen 1969b). The fishery opened for the last time in 1946 when, after complaints from the local fishing industry that fur seals were severely depleting the fish stocks, an open season from 1 June to 30 September was approved for parts of southern South Island, Steward Island, and surrounding islands. No restrictions were placed on age or sex of seals killed, and 6,187 were taken (Sorensen 1969a,b).

The New Zealand Marine Mammal Protection Act of 1978 now gives total protection to all marine mammals within New Zealand and New Zealand's 200-mile exclusive economic zone.

Table 1—Estimates of population size of the New Zealand fur seal within the New Zealand region, from Wilson (1981). The New Zealand mainland consists of North and South Island, Steward Island, Solander Island, and Ruapuke Islands.

Locality	No. fur seals: Estimated total	No. fur seals: Range	Authority
New Zealand mainland	25,500	19,000-35,250	Wilson 1981
Stewart Island	3,300	2,500-4,500	Wilson 1981
North Island	200	100-350	Wilson 1981
Snares Islands	1,150		Crawley 1972
Auckland Islands	1,100	750-1,500	Wilson 1974b
Campbell Island	2,000		Bailey and Sorensen 1962
Antipodes Islands	1,100		Taylor in Sorensen 1969b
Bounty Islands	5,500	5,000-6,000	Falla in Wilson 1981
Macquarie Island	625		Johnstone 1972
Chatham Islands	2,100	1,800-2,700	Wilson 1981
All localities	39,000	30,000-50,000	Wilson 1981

POPULATION SIZE AND TRENDS

Changes in the size and distribution of the New Zealand fur seal population are difficult to quantify because of lack of regular and comparable census data. Fur seal numbers appear to be increasing (Sorensen 1969a; Stonehouse 1965; Taylor 1982; Wilson 1981), though Gaskin (1972) cautioned that at the time any apparent increase might have been due to a redistribution of the existing population.

The most comprehensive population size estimate for New Zealand fur seals within the New Zealand region is 39,000 (range: 30,000-50,000; Wilson 1981; Table 1). This figure is based on direct counts made at colonies between November 1971 and February 1974 and, where necessary, previously published estimates. Counts were made either from the beach, vantage points overlooking individual colonies, or from boats offshore. Count accuracy was estimated in the field and a population size range calculated. Detailed population estimates had previously been made at some colonies (Crawley 1972; Stirling 1968; Wilson 1974a). These data were used by Wilson to adjust his counts for time of year, time of day, and weather conditions. Estimates were thus standardized and are for the total New Zealand region as of January-February 1973.

More recently, Taylor (1982) gave an estimate of 16,000 fur seals at the Bounty Islands based on direct counts, estimates of pup production, and published population parameters of other fur species. This is three times the estimate made by Falla as used by Wilson, and increases Wilson's estimate for fur seals within the New Zealand region to about 50,000.

INFLUENCES

Space and competitors

Considering the probable pre-exploitation population size, space is not a major factor affecting overall population growth. The same can probably be said for food. New Zealand fur seals feed primarily on squid, octopus, and fish (Street 1964). Although New Zealand supports a large commercial squid fishery, there is no indication that squid stocks are being severely reduced. Fur seals in New Zealand have few natural competitors, the most obvious being other seal species, pelagic school fish, and small whales which may compete for the same food resources. Man also competes with seals for squid and fish, but there is no indication that this is having any appreciable effect on fur seal numbers.

Predation

Fur seals within the New Zealand region have no natural terrestrial predators. At sea, they are subject to predation by sharks and killer whales, *Orcinus orca*, (Mattlin 1978a). Fur seal pup remains have been identified in the stomach contents of a male New Zealand sea lion, *Phocarctos hookeri*, collected at the Snares Islands (M. W. Cawthorn, Fish. Res. Div., Wellington, pers. commun.).

Some are caught and drowned accidentally in both trawls and set-nets during commercial fishing operations, but the numbers involved appear to be few and probably are insignificant to the overall population size.

Survivorship

Pup mortality is about 20% from birth to age 50 days and 40% from birth to about age 300 days (Mattlin 1978b). There are no data on postweaning survivorship. Maximum ages determined thus far, based on growth layer counts of canines, are 15 years for males (n=14) and 14+ years for females (n=6; Mattlin 1978a).

REPRODUCTIVE PARAMETERS

Gross examination of ovaries collected from six females aged 4-12+ years suggests that females can bear their first pup by age 5 years (Mattlin 1978a). There are no additional data on age-specific reproduction in females.

Bulls probably attain territorial status at about age 10 years (Mattlin 1978a). This is based on a collection of 10 territorial and nonterritorial bulls collected at Taumaka, Open Bay Islands, from October 1974 to November 1975.

REPRODUCTIVE ECOLOGY

Live births occur on the Open Bay Islands from mid-November through late December, with a mean pupping date of 9-10 December (Mattlin 1981; Miller 1975a). About 77% of births recorded during the 1970-71 breeding season occurred over the 22-day period from 29 November to 19 December (Miller 1975a).

Females are intolerant of other females, and tend to keep a minimum distance of about one body length apart.

The average ratio of territorial bulls to pups was 1:5 on the Snares Islands in 1970 (Crawley and Wilson 1976), 1:6.1 on the Open Bay Islands in 1970-71 (Miller 1975a), and 1:7.3 on the Open Bay Islands in 1974-75 (Mattlin 1978a).

Females remain with their newly born pup for about 9 days (range: 6-12 days) before going to sea to feed for the first time. Early feeding trips are for 1-5 days, though subsequent trips are progressively longer as the pups grow older (McNab and Crawley 1975; Miller 1975a). Time spent ashore between the early feeding trips is about 2-7 days (Miller 1975a). Females suckle their pups for about 300 days, after which they leave the rookery for what is presumed to be an extended feeding trip prior to returning to the rookery to give birth (Crawley and Wilson 1976; Mattlin 1981).

GROWTH

At Open Bay Islands, males have an average birth weight of 3.9 kg (range: 3.25-4.60 kg, $n=7$), females 3.3 kg (range: 2.75-3.80 kg, $n=8$; Mattlin 1981). Growth is greatest within the first 55-60 days following birth, with weight gains of 45-74 g/day for males and 46-61 g/day for females, depending on year (Crawley 1975; Mattlin 1981). From birth to 240 days, both sexes gained about 24 g/day (Crawley 1975). The average weight at age 290 days for 88 males was 14.1 kg (SE$\pm$3.7 kg) and for 79 females 12.6 kg (SE$\pm$3.5 kg; Mattlin 1981).

Adult males may reach 180-200 kg in body weight (Crawley and Wilson 1976; Miller 1975b). The heaviest known recorded weight for a male is 154.1 kg, for a 10-year-old taken at Taumaka, Open Bay Islands in 1975 (Mattlin 1978a). By contrast, the heaviest known recorded weight for a female (minus foetus) is 49.2 kg for a 12+-year-old collected in 1975 at Taumaka (Mattlin 1978a).

FOOD

New Zealand fur seals feed mainly on cephalopods and fish, though they are known to take penguins, particularly at the subantarctic islands (Bailey and Sorensen 1962; Street 1964). Stomach contents of 64 fur seals collected from the east coast, South Island, contained 28.8% octopus, 23.9% squid, 38.1% barracouta (*Thyrsites atun*), and 9.2% other fish by weight (Street 1964). There are few data on the quantities consumed in the wild, though Street calculated an average of 9-10 pounds (4.1-4.5 kg) per meal based on his study of stomach contents. New Zealand fur seals held in captivity at Napier Marineland, Napier, are fed on a diet of mixed fish and squid. Large bulls are fed up to 10 kg per day, large females up to 7.5 kg per day, and small females and immature individuals up to 2.5-3.0 kg per day (K. Newcomb and R. MacDonald, Napier Marineland, pers. commun.).

CITATIONS

BAILEY, A. M., and J. H. SORENSEN.
1962. Subantarctic Campbell Island. Proc., Denver Mus. Nat. Hist. 10, 305 p.

CRAWLEY, M. C.
1972. Distribution and abundance of New Zealand fur seals on the Snares Islands, New Zealand. N.Z. J. Mar. Freshw. Res. 6:115-126.
1975. Growth of New Zealand fur seal pups. N.Z. J. Mar. Freshw. Res. 9:539-545.

CRAWLEY, M. C., and G. J. WILSON.
1976. The natural history and behavior of the New Zealand fur seal (*Arctocephalus forsteri*). Tuatara 22:1-29.

GASKIN, D. E.
1972. Whales, Dolphins and Seals. Heinemann Educational Books Ltd., Auckland, 200 p.

JOHNSTONE, G. W.
1972. A review of biological research by Australian National Antarctic Research Expeditions, 1947-71. Polar Rec. 16:519-32.

McNAB, A. G., and M. C. CRAWLEY.
1975. Mother and pup behavior of the New Zealand fur seal, *Arctocephalus forsteri* (Lesson). Mauri Ora 3:77-88.

McNAB, R.
1907. Murihiku and the Southern Islands. William Smith, Invercargill, 377 p.

MATTLIN, R. H.
1978a. Population biology, thermoregulation and site preference of the New Zealand fur seal, *Arctocephalus forsteri* (Lesson, 1828), on the Open Bay Islands, New Zealand. Unpubl. Ph.D. thesis. Christchurch: Univ. Canterbury, New Zealand, 179 p.
1978b. Pup mortality of the New Zealand fur seal (*Arctocephalus forsteri* Lesson). N.Z. J. Ecol. 1:138-144.
1981. Pup growth of the New Zealand fur seal *Arctocephalus forsteri* on the Open Bay Islands, New Zealand. J. Zool. (Lond.) 193:305-314.

MILLER, E. H.
1975a. Annual cycle of fur seals, *Arctocephalus forsteri* (Lesson), on the Open Bay Islands, New Zealand. Pac. Sci. 29:139-152.
1975b. Body and organ measurements of fur seals, *Arctocephalus forsteri* (Lesson), from New Zealand. J. Mammal. 56:511-513.

MORRELL, B.
1832. A narrative of four voyages to the southern seas, north and south Pacific Ocean, Chinese Sea, Ethiopia and southern Atlantic Ocean, Indian and Antarctic Ocean from the year 1822 to 1831. J. & J. Harper, New York, 492 p.

SORENSEN, J. H.
1969a. New Zealand seals with special reference to the fur seal. N.Z. Mar. Dep. Fish. Tech. Rep. 39, 35 p.
(editor) 1969b. New Zealand fur seals with special reference to the 1946 open season. N.Z. Mar. Dep. Fish. Tech. Rep. 42, 80 p.

STIRLING, I.
1968. Diurnal movements of the New Zealand fur seal at Kaikoura. N.Z. J. Mar. Freshw. Res. 2:375-377.

STONEHOUSE, B.
1965. Marine birds and mammals at Kaikoura. Proc. N.Z. Ecol. Soc. 12:13-20.

STREET, R. J.
1964. Feeding habits of the New Zealand fur seal. N.Z. Mar. Dep. Fish. Tech. Rep. 9, 20 p.

TAYLOR, R. H.
1982. New Zealand fur seals at the Bounty Islands. N.Z. J. Mar. Freshw. Res. 16:1-9.

WILSON, G. J.
1974a. Distribution, abundance and population characteristics of the New Zealand fur seal (*Arctocephalus forsteri*). Unpubl. M.Sc. thesis. Christchurch: Univ. Canterbury, New Zealand, 204 p.
1974b. A preliminary report on the distribution and abundance of the New Zealand fur seal (*Arctocephalus forsteri*) at the Auckland Islands December 8, 1972 to January 15, 1973. N.Z. Min. Agricult. Fish., Fish. Tech. Rep. 133, 20 p.
1981. Distribution and abundance of the New Zealand fur seal, *Arctocephalus forsteri*. N.Z. Fish. Res. Div. Occas. Publ. 20, 39 p.

New Zealand Fur Seal, *Arctocephalus forsteri*, (Lesson), in South Australia

JOHN K. LING
South Australian Museum
North Terrace
Adelaide 5000
Australia

INTRODUCTION

Resident fur seals inhabiting southern Australia have only recently been recognized as two allopatric species: *Arctocephalus pusillus doriferus*, the Australian fur seal in the southeast, and *A. forsteri*, the New Zealand fur seal in the west (King 1969; Repenning et al. 1971). Soon after the discovery of seals in eastern Bass Strait by Matthew Flinders in 1798, sealing gangs set out to exploit these herds. Over the next 40 years, sealing took place along the entire southern coast of Australia as far west as the islands of the Recherche Archipelago off southern Western Australia.

Both fur seals and sea lions (hair seals), *Neophoca cinerea*, were exploited. The pelts were landed at either Hobart or Sydney for transshipment, or were taken directly by British or American sealing vessels to Europe or the Orient.

Records are therefore exceedingly difficult to analyze to give a true picture of the extent of the harvest or the pristine state of the seal populations. Indeed, the exact identity of the species taken can only be surmised. We know from Flinders (1814), a most perceptive observer, that hair seals and fur seals inhabited eastern Bass Strait in 1798. We can only assume, however, that the fur seals then were the same species as, and occupied a similar range to, the resident species today. Sea lions now occur only west of Bass Strait.

HISTORY OF HARVESTING

Though not exhaustive, secondary sources of information pertaining to seal skin cargoes landed by vessels in Hobart or Sydney between 1804 and 1834 reveal that at least 70,400 fur seal skins were taken from Kangaroo Island, South Australia, and possibly other islands west of Bass Strait (Fig. 1). There is no evidence to suggest that the harvesting was anything but indiscriminate.

By contrast, the same sources show that at least 143,000 fur seal skins were taken from southeastern Australia and some 300,000 from Macquarie Island and other subantarctic islands.

It is interesting, therefore, to compare the currently estimated sizes of the *A. p. doriferus* and *A. forsteri* populations in their respective ranges: 20,000 and "several thousand" (Warneke 1982). Abbott (1979) says that there are only 400-500 *A. forsteri* in Western Australia, and my estimate is that several thousand inhabit South Australia.

DISTRIBUTION

The New Zealand fur seal occurs on offshore islands in South and Western Australia (Fig. 2). There are no known mainland colonies. The largest colonies currently appear to be at Cape du Couedic at the western end of Kangaroo Island and the South Neptune Islands at the foot of Spencer Gulf, where up to a thousand fur seals haul out. In addition, there are many other sites where smaller numbers ranging from about a dozen to (rarely) a few hundred fur seals have been recorded. But the exact status of any of these colonies is not presently known because detailed research is not now being undertaken. Likewise, interchange between haul-out sites over long or short distances, e.g., South Australia to Western Australia, has not been investigated by tagging experiments.

Warneke (1982) cites historical evidence that the New Zealand fur seal extended to the Furneaux Group in eastern Bass Strait, but it is believed not to occur today east of about long. 148°E. In

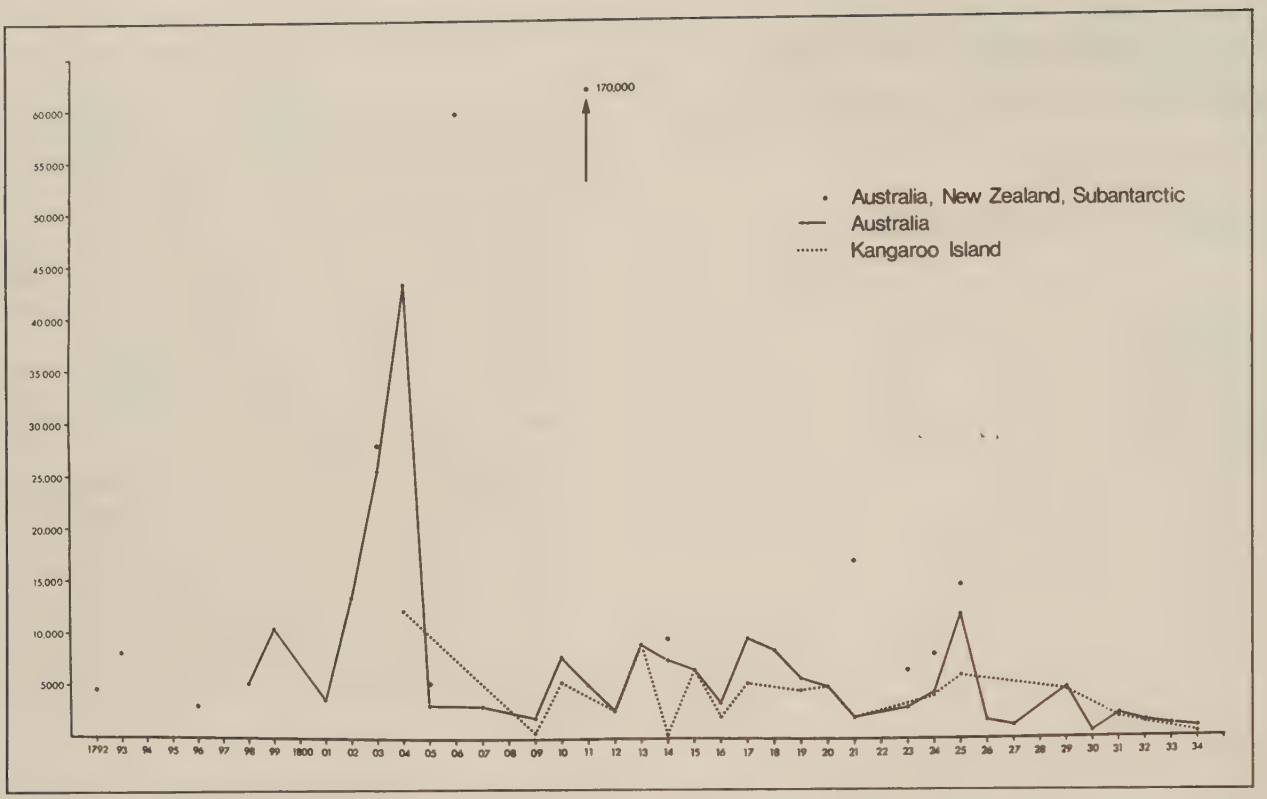


Figure 1—Cargos of seal skin from Australasian sealing grounds, 1792-1834 (from various sources). Only the Kangaroo Island figures are relevant to this report.

Western Australia *A. forsteri* has declined in range and abundance, being now extinct between Cape Leeuwin and Eclipse Island (Abbott 1979). Thus there has been a contraction of the range of this species which now extends from the Recherche Archipelago to western Bass Strait.

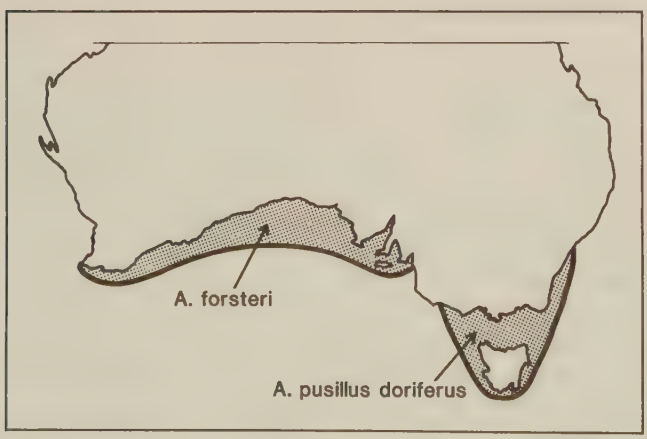


Figure 2—Distribution of fur seals *Arctocephalus forsteri* and *A. pusillus doriferus* in Australia.

POPULATION SIZE AND TRENDS

The total Australian population of *A. forsteri* is estimated to be about 5,000 or less.

The only regular censuses in recent years have been carried out at Cape du Couedic at the western end of Kangaroo Island. Fur seals haul out on a rocky platform below the cliffs near the Cape and can also be seen on the landward side of the innermost of the two Casuarina Islets 300 and 2,000 meters SSW of the Cape. Although regular counts have not been made in recent years, trends are indicated in Figure 3. Fur seals hauling out during the period of the regular counts (1975-78) consisted mainly of either immature animals or females. A few males were seen, as were some small black pups, but no attempts were made to carry out classified censuses; only crude totals were recorded.

As recently as March and again in June 1983, several small black pups were seen being suckled and a number of mature bulls were also observed. No fighting or other manifestation of territorial behavior was apparent. (The breeding season is believed to be in December and January.) Their average size was such that the vast majority of fur seals could have been either immature animals of either sex or mature females.

Nevertheless, April 1983 is the first time suckling females and adult bulls have been seen at Cape du Couedic in such numbers as to suggest that this area may be assuming the status of a breeding site. It has been previously suggested that it may be the site to which immature animals disperse, driven away from a breeding site (possibly the Neptune Islands) when the next generation of pups is born.

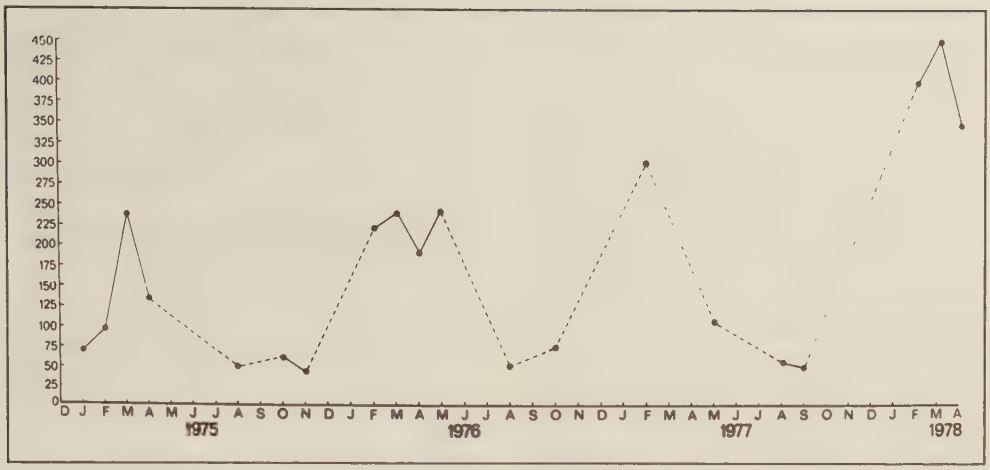


Figure 3—New Zealand fur seal counts at Cape du Couedic, Kangaroo Island, South Australia: 1975-78. Actual counts made only where shown by dots.

These are extremely recent or short-term changes. It cannot be inferred that they represent any long-term population trends or indeed did not occur previously even on several occasions. Moreover, the Cape Du Couedic population should not be regarded in isolation from the other presumed major breeding site at the South Neptunes.

These very crude data merely confirm that much more extensive, intensive, and expensive study needs to be carried out before the basic population questions can be answered. Thus, some pertinent information on *A. forsteri* in southern Australia is unavailable at present.

CITATIONS

ABBOTT, I.
1979. The past and present distribution of sea lions and fur seals in Western Australia. Rec. West. Aust. Mus. 7:375-390.

FLINDERS, M.
1814. A Voyage to Terra Australis. (Two volumes and folio atlas) G. and W. Nicol, London, 613 p.

KING, J. E.
1969. The identity of the fur seals of Australia. Aust. J. Zool. 17:841-853.

REPENNING, C. A., R. S. PETERSON, and C. L. HUBBS.
1971. Contributions to the systematics of the southern fur seals, with particular reference to the San Juan Fernandez and Guadalupe species. Antarct. Res. Ser. 18:1-34.

WARNEKE, R. M.
1982. The distribution and abundance of seals in the Australasian region, with summaries of biology and current research. *In* Mammals of the Seas, p. 431-475. FAO Fish. Ser. 5, Vol. 4.

Subantarctic Fur Seal, *Arctocephalus tropicalis*, at Gough Island (Tristan Da Cunha Group)

MARTHAN N. BESTER
Mammal Research Institute
University of Pretoria
Pretoria 0002
South Africa

HISTORY OF HARVESTING

The following picture emerged from consulting Swales (1956) and Wace and Holdgate (1976). Discovered in 1505, Gough Island showed no clear evidence of any previous human visitors. Marine life, including elephant seals (''sea lions as large as oxen''), fur seals (''sea-wolfs''), and whales, was extremely abundant (at the Tristan group) and was commented on by visitors between 1655 and 1696.

American sealers commenced operations at Tristan da Cunha itself in 1790 when John Patton of the vessel *Industry* spent nine months obtaining 5,600 fur seal pelts. Sealing gangs lived on the islands for considerable periods, clubbing and skinning the fur seals and salting the pelts for later collection by their company's vessels en route to the Northern Hemisphere markets in America, Europe, and China. A gang of ten men discovered by HMS *Nereus* on Gough Island in 1811 had been there for 18 months, and may have taken some 1,100 fur seal skins that year. After about 1820 fur sealing in the islands declined due to overexploitation of stocks. By 1829 it was remarked that Gough Island ''used to abound in seal. . .but they have now sought more distant resorts''.

A resurgence of sealing took place between 1860 and 1890 at the Tristan islands. In 1881, 151 skins were taken, probably all from Gough Island, but a party which spent 18 months there in 1888-90 took only 311 fur seals (and one elephant seal). A second party in 1891-92 found the seals were so reduced in numbers that the industry ended. Sealing up to this point was indiscriminate.

Since 1892 the fur seals have remained virtually undisturbed. In several years (four, perhaps more) before 1955-56, and coincidental with the start of commercial crawfishing operations in 1951, up to 400 fur seals were taken illegally each year. This sealing was not indiscriminate, but concentrated mainly on immatures of both sexes. Since then a few hundred (?) have been taken by the fishing company under permit from the Tristan Administration.

It is impossible to make a reasonable estimate of the total numbers of seals taken since 1790 from the island(s) during the course of sealing activities.

From November 1977 to October 1978, 74 adult males, 75 adult females, 41 immature males, 16 immature females, and 14 pups (9 males + 5 females) were culled as part of a research program.

POPULATION SIZE AND TRENDS

Fifty-three percent of the approximately 41 km coastline was counted during the 1977-78 summer by two observers searching for pups on foot using direct methods, and the remaining seals were counted by a single observer from elevated vantage points on and behind beaches prior to pup searches. All the seals counted were allocated to the following categories: adult males (AM), adult females (AF), immatures and subadults of both sexes (SUB), unclassified (UNCL), and pups.

Seals on the idle, nonbreeding, and breeding colony sites (Bester 1982) were counted during the peak haulout and immediately thereafter (20 December to 3 January). Established breeding colony sites were counted after the pupping season when pups were still confined to the beaches (29 January to 5 February). The following count corrections were made:

1. Fur seal numbers on three inaccessible beaches within the census area were estimated according to the numbers on two other sites similar in area and topography.

2. For four beaches not revisited during 1977-78, the 1975-76 counts (Bester 1980) were used.

3. The reduced number of adult males that were counted after the pupping season on breeding colony sites were adjusted upward according to the known amount of post-breeding season decrease (72%) on other breeding colony sites (Bester 1981).

4. Pup counts (representing the total number of pups born on all beaches counted) were corrected for undercounting (33%). The correction was based on counts made before and during an exhaustive search of pups for tagging on each of two breeding colony sites, which were physiognomically typical of the beaches where only pups were counted.

5. On established breeding colony sites where only pups were counted, adult male numbers were calculated using the formula pup numbers/male:pup ratio (the latter ratio was 1:6.6 using corrected pup counts; Bester 1977). Female numbers were estimated from corrected pup counts (females normally bear only one pup). On breeding colony sites (December) actual counts of females were used only when they exceeded the total number of pups born there.

6. A population figure for the whole island was calculated through extrapolation from the censused east and southwest coast sectors. The southwest coast resembled the uncensused northwest side physiognomically and biologically (both sectors were popular pupping sites; Swales 1956; Bester 1982). The northwest and southwest coasts form respectively 31.0 and 19.3% of the total coastline (ratio 1.61:1). Similarly, the eastern sector resembled the northeastern sector in being frequented by nonbreeders (Swales 1956; Bester 1982). These areas formed respectively 34.0 and 15.7% of the total coastline (ratio 1:0.46).

7. The numbers of non-pregnant females, and year-old seals which were absent from the island during the breeding season (Bester 1981) were estimated by assuming a pregnancy rate of 86.0% (from *A. gazella*, Payne 1977) and a mortality rate of 23.9% to 1 year of age (the mortality rate of *A. gazella* at South Georgia in 1976-77). The use of *A. gazella* values is based on a similar rate of annual increase, 15.9%, in the two species.

8. Observations since 1974-75 showed a pup mortality figure of 10% by the end of January and this figure was subtracted from the population estimate.

The extrapolated population size during January/February 1978 is shown in Table 1 (Bester 1980).

Using pup counts, and the expression $N_t = N_o e^{rt}$ (Caughley 1977), the instantaneous coefficient of population growth, designated by the symbol r, is calculated as 0.159 (N_o = 484; N_t = 15,884; t = 22) or 0.172 (N_o = 484; N_t = 21,179 adjusted, t = 22). This indicates an estimated mean increase of 15.9% per year on the censused area since 1955 and 12.6% (N_o = 2,754; N_t = 44,230; t = 22) or 13.9% (N_o = 2,754; N_t = 58,973 adjusted; t = 22) for the whold island (extrapolated) up to 1977-78 (Bester 1980).

INFLUENCES

Space

The reduction in the rate of population increase on preferred southwest coast beaches (Snug Harbour to Repetto Bay South) from 14.8% per year before 1975-76 (N_o = 296; N_t = 5,684; t = 20) to 10.2% thereafter (N_o = 5,684; N_t = 6,972; t = 2), and the reluctance of pregnant females to pup on eastcoast beaches because of their specific habitat requirements (Bester 1982), show that optimum breeding space is becoming limited. A further drop in the rate of increase (to 6.6%) occurred on three southwest coast beaches (Point Bay to Repetto Bay South) between 1977-78 and 1980-81 (N_o = 4,442; N_t = 5,417; t = 3). The continued relatively high growth rate of the Gough Island population therefore apparently depends on the ability of pregnant females to exploit less suitable eastcoast open beaches, which were densely populated by nonbreeders (mostly males) during the 1977-78 breeding season. This had not occurred by the 1980-81 summer.

Food

No quantitative data are available on the size of the food base used by *A. tropicalis* in the region of Gough Island.

Competitors

The small population (<200) of elephant seal, *Mirounga leonina*, is spatially and temporally separated from *A. tropicalis* on land, especially during their respective breeding seasons (Bester 1980). Possible competition between these species for a common food base is of no consequence to the fur seals.

Table 1—Extrapolated population size of *Arctocephalus tropicalis* at Gough Island during January-February 1978.

Sector	Adult males	Adult females	Immatures and subadults (both sexes)	Pups		Unclassified	Total
Southwest	3,500	22,405	46	(16,802)*	22,405	0	48,356
Northwest** (× 1.61)	5,635	36,072	74	(27,051)	36,072	0	77,853
East	8,227	1,068	10,295	(258)	340	1,236	21,166
Northeast** (× 0.46)	3,784	491	4,736	(119)	156	569	9,736
Subtotal	21,146	60,036	15,151	(44,230)	58,973	1,805	157,111
Total***	21,146	69,636	53,432	(39,807)	53,076	1,805	199,095

*Uncorrected pup counts in parentheses.
**For explanation of calculation, see text.
***Subtotal + 9,600 nonpregnant females and 38,281 absent 1-year-olds, minus 5,897 dead pups.

Commercial crayfishing operations around Gough (and other Tristan Islands) constitute no threat to fur seals, because crayfish, *Jasus tristani*, are not a major dietary item (Bester and Laycock 1985).

Sperm whales *Physeter catodon* and southern right whales *Eubalaena australis* were intensively hunted in Tristan waters between 1830 and 1870; the latter were hunted again (illegally) in 1963 by a Russian whaling fleet (Wace and Holdgate 1976). The present status of whales in this area is unknown, and their effect on the food base (directly or indirectly) is probably insignificant.

PREDATORS

Killer whales, *Orcinus orca*, sightings are rare, and a leopard seal, *Hydrurga leptonyx*, was reported only once at Gough Island (P. Warren, pers. commun.). Blue sharks, *Prionace glauca*, also occur at Gough Island. The effect of these potential predators on the fur seals is unknown, but is probably insignificant.

SURVIVORSHIP

Pup mortality during approximately the first 6 weeks of life is 10% (Bester 1980). Longevity of males and females is 18+ and 23+ years, respectively. No other information is available.

REPRODUCTIVE PARAMETERS

No information is available on the proportion of a cohort that pups first at each age. Females attain sexual maturity (first ovulation) at 4-6 years of age; 42% at age 4 ($n=12$), and 79% at age 5 ($n=14$).

A sample of 84 females of 2 years of age or more at the last breeding season was examined for pregnancy after implantation and before the next ovulation ($n=38$) and, through back calculation, reproductive condition during the preceding year ($n=90$). Sex ratio at birth is taken as 1:1, and litter size as 1. Delayed implantation lasts for about 128 days with implantation occurring during the second half of April. The fecundity schedule for the females is shown in Table 2.

Based on the presence of spermatoza in the epididymidal tubules from 22 September to 21 February when all adult males are reproductively active, males reach sexual maturity between 3 and 4 years of age. Secondary sexual characteristics are only fully developed in males older than 7 years of age. Therefore, adult territorial males within breeding aggregations (not sampled) appeared to be at least 8 years old. All adult males are reproductively quiescent during the winter (May to July).

REPRODUCTIVE ECOLOGY

Median birth dates, calculated indirectly using a simplified probit analysis (Caughley 1977), were 9 December and 13 December during 1974 and 1975, respectively. Births are spread over approximately 6 weeks from 21 November (earliest recorded birth) to the first week in January.

No information is available on the density of females (females/m^2) during the peak breeding season and gregariousness. The degree of polygyny, expressed as territorial male/pup ratio, at established breeding colony sites is 1:5.3 (uncorrected) or 1:6.6 (corrected for undercounting pups). A maximum of 14 females occurred within the territory of a male at any one time.

Table 2—Age-specific fecundity schedule for female *A. tropicalis* at Gough Island.

Age	Sample size f_x	No. pregnant B_x	Female births per female m_x
1	5	0	0.00
2	9	0	0.00
3	9	0	0.00
4	12	5	0.21
5	9	7	0.39
6	8	8	0.50
7	14	14	0.50
8	7	7	0.50
9	12	11	0.46
10	13	13	0.50
11	6	6	0.50
12	9	7	0.39
13	3	2	0.33
13+	12	3	0.13

The precise attendance patterns of females, duration of trips to sea, and visits ashore are unknown. The lactation period lasts 10-11 months, and pups may suckle (on-nipple time) for bouts of 21.4±20.5 min ($\bar{x}\pm$SD, $n=15$) at intervals ($n=7$) of 1.2±0.44 h (three female-pup pairs observed over 1 day) at Gough Island (Bester and Kerley 1983).

GROWTH

During 1975-76 the mean weight (kg) of pups less than 1 week old was 4.4±0.9 ($\bar{x}\pm$SD) and 4.0±0.8 for males ($n=7$) and females ($n=6$) respectively. During 25-30 October 1980, male and female underyearlings, presumably recently weaned, weighed 12.9±2.2 kg ($n=12$) and 9.5±1.8 kg ($n=8$), respectively. Growth rates of pup cohorts are not available.

The mean weight of adult non-pregnant females older than 6 years of age was 35.6±4.5 kg ($n=29$) ranging from 28.0 to 46.0 kg. Eight adult, nonterritorial males older than 9 years of age and in excellent condition were collected at an idle colony site from 19 November to 10 December and weighed an average 131.3±20.0 kg (range 97.0-158.0 kg).

FOOD

A. tropicalis at Gough Island preys predominantly on cephalopods, but also takes relatively small quantities of fish (unidentified). Stomachs of fur seals ($n=220$) culled on land were either empty (32%), contained only stones (8%), or contained almost exclusively prey remains that were resistant to digestion, such as cephalopod pens, beaks, eye-balls, and fish bones and otoliths. The pooled cephalopod lower beak ($n=424$), that could be identified ($n=337$), showed that Ommastrephidae (52.5%), Histioteuthidae (25.2%), Onychoteuthidae (19.9%), Cranchiidae (2.1%), and Octopoteuthidae (0.3%) constituted the main prey items based on frequency of occurrence. Cephalopod mass estimates, from regression of lower rostral lengths against mass, approximated this relative arrangement of cephalopod families as shown in Table 3 (taken from Bester and Laycock 1985).

Table 3—Cephalopod lower beaks identified from stomach contents of *A. tropicalis* showing their relative importance by number and reconstituted mass.

Family	Species	No.	%	Mean lower rostral length (mm)	Mean wt. (kg)	Total estimated mass (kg)	Total estimated mass (%)	Family Contribution (%) by no.	Family Contribution (%) by mass
Ommastrephidae	(?) *Todarodes* A	95	28.2	5.5	0.290	27.6	28.3	52.5	95.7
	Todarodes B	10	3.0	6.3	0.430	4.3	4.3		
	Todarodes (A or B)	17	5.0	6.6	0.480	8.2	8.4		
	Ommastrephid sp. A	50	14.8	8.3	0.950	47.5	48.7		
	Ommastrephid sp. B	5	1.5	10.1	1.160	5.8	5.9		
Histioteuthidae	Histioteuthid type 8	83	24.6	1.9	0.021	1.7	1.7	25.2	2.3
	(?) *Histioteuthis*	2	0.6	2.3	0.240	0.5	0.5		
Cranchiidae	*Galiteuthis armata*	1	0.3	2.8	0.030	<0.1	<0.1	2.1	0.4
	Bathothauma lyromma	2	0.6	3.4	0.045	0.1	0.1		
	Cranchiid sp.	4	1.2	1.5	0.079	0.3	0.3		
Onychoteuthidae	*Moroteuthis knipovitchi*	6	1.8	4.5	0.160	1.0	1.0	19.0	1.5
	(?) *Moroteuthis* sp.	61	18.1	1.6	0.008	0.6	0.5		
Octopoteuthidae	Octopoteuthid sp.	1	0.3	2.6	1.109	0.1	0.1	0.3	0.1

CITATIONS

BESTER, M. N.

1977. Habitat selection, seasonal population changes, and behaviour of the Amsterdam Island fur seal *Arctocephalus tropicalis* on Gough Island. D.Sc. thesis, Univ. Pretoria, 193 p.

1980. Population increase in the Amsterdam Island fur seal *Arctocephalus tropicalis* at Gough Island. S. Afr. J. Zool. 15:229-234.

1981. Seasonal changes in the population composition of the fur seal *Arctocephalus tropicalis* at Gough Island. S. Afr. J. Wildl. Res. 11:49-55.

1982. Distribution, habitat selection and colony types of the Amsterdam Island fur seal *Arctocephalus tropicalis* at Gough Island. J. Zool. (Lond.) 196:217-231.

BESTER, M. N., and G. I. H. KERLEY.

1983. Rearing of twin pups to weaning by subantarctic fur seal *Arctocephalus tropicalis* female. S. Afr. J. Wildl. Res. 13:86-87.

BESTER, M. N., and P. A. LAYCOCK.

1985. Cephalopod prey of the fur seal *Arctocephalus tropicalis* at Gough Island. *In* Siegfried, W. R., P. R. Condy, and R. M. Laws (eds.), Nutrient cycling and food webs in the Antarctic: Proceedings of the Fourth SCAR Symposium on Antarctic Biology, p. 551-554. Springer-Verlag, Berlin.

CAUGHLEY, G.

1977. Analysis of vertebrate populations. John Wiley, New York, 234 p.

PAYNE, M. R.

1977. Growth of a fur seal population. Phil. Trans. R. Soc. Lond. B. 279:67-79.

SWALES, M. K.

1956. The fur seals of Gough Island. Unpubl. rep., Colonial Office, London, 13 p.

WACE, N. M., and M. W. HOLDGATE.

1976. Man and nature in the Tristan da Cunha Islands. IUCN Publ. New Ser. Suppl. pap.

Arctocephalus tropicalis on the Prince Edward Islands

GRAHAM I. H. KERLEY[1]
Mammal Research Institute
University of Pretoria
Pretoria 0002
South Africa

INTRODUCTION

When the first scientific expedition, the Challenger Expedition, visited the Prince Edward Islands in 1872 they found no fur seals. In 1951-52 Rand (1956) made the first estimates of the fur seal population size and collected some specimens there. The next population estimate was that of De Villiers and Ross (1976) in 1972-73. Condy presented population estimates for 1974-1975, seasonal haulout cycles, fluctuations in biomass, annual food consumption (Condy 1978, 1981), and the structure of the fur seal pelage (Condy and Green 1980). I studied the interrelationships between the two species of fur seals there, the subantarctic fur seal *Arctocephalus tropicalis* and the Antarctic fur seal *A. gazella* (Bester and Kerley 1983; Kerley 1981, 1983a,b,c, 1985; Kerley and Bester 1983) during the 1980-81 and 1981-82 austral summers. Pinniped research at the Prince Edward Islands is carried out under the auspices of the Mammal Research Institute, University of Pretoria. The tagging program initiated in the early seventies (Condy and Bester 1975) is being maintained.

HISTORY OF HARVESTING

The Prince Edward Islands were discovered in 1772, and within 30 years the *A. tropicalis* population there was being intensively exploited. By 1802 sealers were camping on both islands and the fur seal population was soon decimated (Marsh 1948). The Challenger Expedition failed to locate any fur seals there, probably because expedition members landed on a beach that was not occupied by fur seals, and not because none existed on the islands. The South African firm Irving and Johnstone was the major sealing organization active at the Prince Edward Islands (Marsh 1948) but, unfortunately, their records have been destroyed. The last successful fur sealing expedition to the Prince Edward Islands was carried out in the 1920-21 austral summer when 785 pelts were harvested (Anonymous 1921); the SS *Kildalkey* elephant sealing expedition of 1931 (Marsh 1948) may have collected some fur seals. Since 1948 the Islands' fauna and flora have been protected, and the only harvest allowed was for scientific purposes.

POPULATION SIZE

The population size of *A. tropicalis* at the Prince Edward Islands was estimated during the 1981-82 austral summer using adjusted, direct counts (Kerley 1983a). The coastline of Marion Island was censused from 26 January to 3 February 1982 (Table 1). Pup numbers were adjusted for undercounting (16% of the total present) to yield an estimate of live pups. This estimate was further adjusted to account for pup mortality to the census date (7.0%) and assumed pregnancy rates (86%) to yield an estimate of the number of females present. Because counts were not conducted during the peak fur seal haulout, the counts of adult males and immatures (older than 1 year) were adjusted by 83% and 29%, respectively, to compensate for known decreases from peak haulout to the date of the census (Kerley 1983b). Yearlings were absent from the Island during the census and were estimated from the previous year's pup production (censused during 1980-81) using an estimated mortality to age 1 year of 23.9% (from *A. gazella* at South Georgia; Payne 1977). The total *A. tropicalis* population on Marion Island was estimated to be 19,857 (Kerley 1983a).

[1]Present address: Dept. of Zoology, University of Port Elizabeth, P.O. Box 1600, Port Elizabeth 6001, RSA.

Table 1—Numbers of *A. tropicalis* counted on the Prince Edward Islands during the 1980-81 and 1981-82 austral summers, with adjusted totals. See text for details of adjustments.

	Adult				
	Males	Females	Pups	Immatures	Adjusted totals
Marion Island					
Unadjusted	856	2,384	3,193	2,516	
Adjusted	5,244	4,768	3,813	3,554 + yearlings	19,857
Prince Edward					
Unadjusted	203	742	2,300	852	
Adjusted	—	—	3,030	—	14,761
Total					34,618

The censuses of Prince Edward Island (Table 1) were carried out after the summer peak in *A. tropicalis* numbers. The population there was estimated from the ratio of births: total numbers (1:4.8) found on Marion Island. The estimated number of births was derived from the pup counts adjusted for undercounting and using a mortality figure of 9.4% to compensate for the later census date. The total population of *A. tropicalis* on Prince Edward Island was estimated to be 14,761 seals, or a total of 34,528 seals on both islands.

POPULATION TRENDS

The annual rates of population increase for Marion Island were calculated using data in Rand (1956), Condy (1978), and Kerley (1983a). Between 1951-52 and 1974-75 the total Marion Island fur seal population increased by 11% per year (N_o=500, N_t=7,000, t=23; Condy 1978) while pup numbers increased by 10% per year (N_o=167, N_t=1,666; Condy 1978). Due to the likelihood that Rand's (1956) population estimates were low, these rates of increase are overestimates. Between 1974-75 and 1981-82 the total estimated *A. tropicalis* population on Marion Island increased by 14.9% per year (N_o=7,000, N_t=19,857, t=7; Kerley 1983a) while unadjusted pup numbers increased by 15.0% (N_o=1,115, N_t=3,193; Kerley 1983a). Between 1980-81 and 1981-82, comparable, unadjusted *A. tropicalis* pup numbers showed an extremely high increase of 23%, indicating that the annual rate of increase for this population is increasing, apparently following a steep sigmoid growth pattern. Unfortunately, there are no historical data on which to base similar estimates for Prince Edward Island.

INFLUENCES ON POPULATION SIZE AND TRENDS

The high rate of population increase shown for the Marion Island *A. tropicalis* population suggests that density-dependent factors, such as breeding space and food resources especially for lactating cows, are at present not limiting. On high-density traditional fur seal beaches, lower-than-average rates of increase were found. However, this is probably a result of emigration of fur seals to neighboring, less crowded beaches (Kerley 1983a). At present, although the west coast beaches of Marion Island are extensively utilized, breeding space there does not appear to be limiting, while the east coast beaches are poorly utilized.

It is not possible to make any assumptions about the influences of food resources on population trends. Although fish, cephalopods and euphausids form the diet of Marion Island *A. tropicalis* (Rand 1956; Condy 1978, pers. observ.), these trophic relationships are poorly understood. Furthermore, it is not known whether the diet of the fur seals at their pelagic feeding grounds (presumably in the vicinity of the Antarctic Convergence; Condy 1978) bears any relation to the stomach contents of seals killed on land.

Although there is a small population of *A. gazella* present at the Prince Edward Islands (Kerley 1983a), the effects of competition between these two species are unknown. Competition for breeding space is reduced by differences in their preferred breeding habitat (Kerley 1984). Similarly, competition for breeding space between fur seals and elephant seals *Mirounga leonina* is reduced by differences in habitat preferences and seasonal haulout patterns (Condy 1978). It is not known to what extent the fur seals compete with large populations of seabirds for space or food. As there are no major fisheries in the vicinity of the Prince Edward Islands, it is doubtful whether any competition exists between fur seals and man.

Although killer whales, *Orcinus orca*, are common at the Prince Edward Islands, where they prey on penguins and elephant seals (Condy et al. 1978), no predation by killer whales on fur seals was observed. Fur seals were occasionally seen swiming within a few meters of killer whales without showing any apparent concern (pers. observ.). Predation by giant petrels, *Macronectes* spp., and skuas, *Catharacta* sp., is generally limited to moribund fur seal pups.

Nearly all adult fur seals inspected contained unidentified nematodes in their stomachs and cestode cysts in their blubber. An unidentified louse species was found to have caused mange in one specimen (unpubl. data).

SURVIVORSHIP

Survivorship data are available only for pups. Pup mortality estimates are obtained by regular searches of a beach for pup carcases. The pup mortality to a median age of 86 days (10.2%) is possibly an underestimate, since an unknown proportion of pup carcasses could have fallen unnoticed into crevasses in the rocks or been washed away (unpubl. data).

REPRODUCTIVE PARAMETERS

Very little information is available regarding the reproductive parameters of the Prince Edward Island *A. tropicalis* population. The sex ratio of tagged pups (age ± 2 months) did not differ significantly from unity (n=1,383; χ^2=0.1627). A possible case of successful twinning by an *A. tropicalis* female was reported by Bester and Kerley (1983).

REPRODUCTIVE ECOLOGY

A. tropicalis pups at the Prince Edward Islands are born from the beginning of December to the second week of January, excluding a few premature and/or late births. The median date of birth, calculated indirectly using a simplified probit analysis, was 17 December with a standard deviation for the season of births of 19.1 days (Kerley 1983b).

The intragroup density of fur seals at peak breeding season is not known for the Prince Edward Islands *A. tropicalis* population,

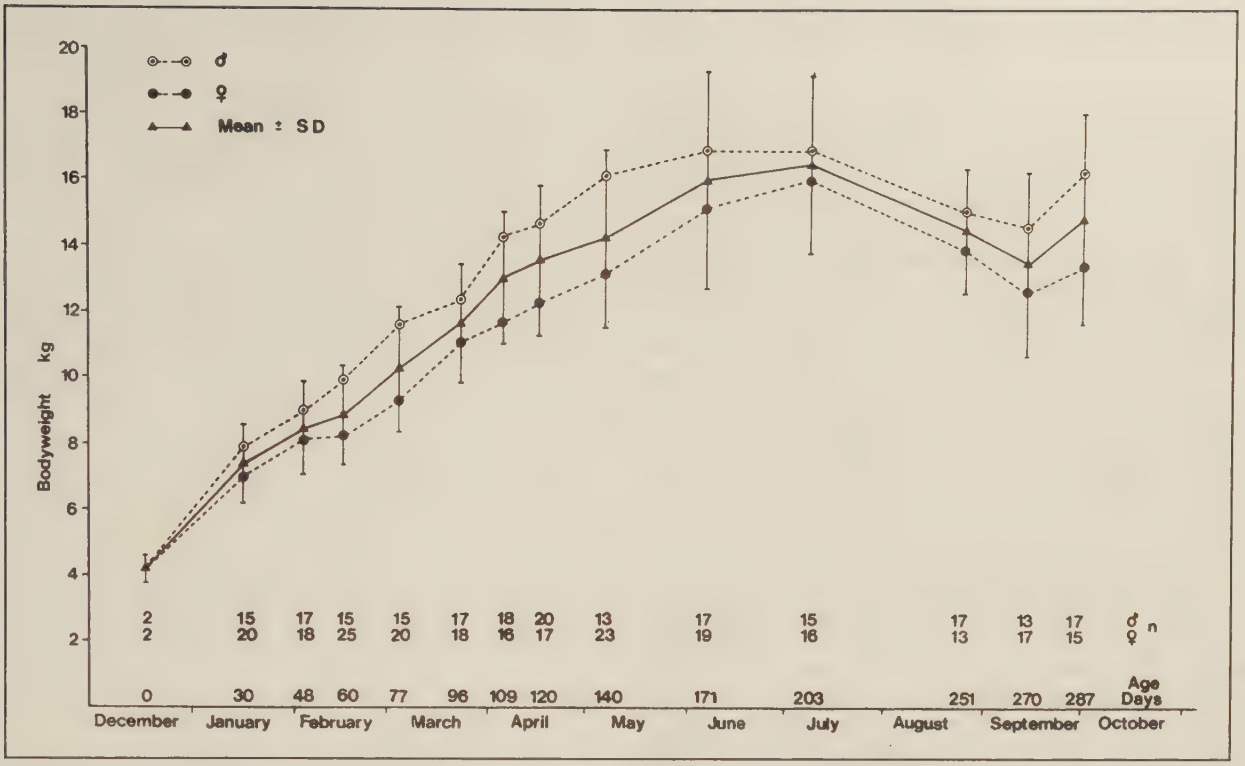


Figure 1—Growth from birth to weaning of *Arctocephalus tropicalis* at Marion Island (Kerley 1985).

and would be difficult to estimate due to the rugged nature of the preferred breeding habitat. An estimate of the degree of polygyny calculated for the Cliff Beach Study Colony is 2.4 pups/male, using the highest number of adult males recorded at peak breeding season and the adjusted estimate of pup numbers (Kerley 1983a,b).

The maximum length of the lactation period for *A. tropicalis* at the Prince Edward Islands has been estimated to be 300 days (Kerley 1983b), although pup growth data suggest that the lactation period may be as short as 260 days (Kerley 1985).

GROWTH

The mean birthweight, calculated for two males and two females, was 4.2 ± 0.4 kg ($\bar{x}$±SD) and weaning weights were 16.4 kg and 13.5 kg for males and females, respectively (Kerley 1985). Pup growth is linear for the first 120 days and is described by the function: Mass (kg) = 4.99 + 0.072 Age (days). Thereafter, growth slowed. Pups attained maximum weight in July at the age of 203 days (Fig. 1), then lost weight, and recovered perceptibly at the end of September.

The largest *A. tropicalis* adult male collected on Marion Island weighed 117.5 kg, but the average weight, 88.3 ± 15.7 kg ($\bar{x}$±SD, n=18) was considerably less. Adult females were much smaller (mass = 34.1 ± 8.2 kg, n=4).

DIET

As mentioned earlier, it is uncertain to what extent the stomach contents of fur seals hauled out on land bear any relation to their pelagic diet. Rand (1956) reported that the stomachs of fur seals collected on Marion Island contained mostly fish (Notothenidae—inshore, benthic), cephalopods, and euphausids. Condy (1981) recorded cephalopod beaks, fish remains, penguin feathers, seaweed, and stones as stomach contents, and assumed that the fur seal's overall diet consisted of 50% cephalopods, 45% fish, and 5% euphausids. Material from stomach contents collected by Condy (1981) and the author are at present being identified by the Prey Identification Service at the Port Elizabeth Museum, R.S.A.

CONCLUSIONS

Although the Prince Edward Islands have a relatively accessible and robust fur seal population, it is poorly understood. The continued increase of this population presents a number of research opportunities in the biology of fur seals, and these opportunities should be exploited whenever possible. Efforts should be made to relate this with other *A. tropicalis* populations that are at different stages of population expansion (Gough, Amsterdam, and Crozet Islands) as well as with the sympatric population of *A. gazella*.

CITATIONS

ANONYMOUS.

1921. Back from Kerguelen. Voyage of SS *Karatora*. Cape Argus, 21 March 1921.

BESTER, M. N., and G. I. H. KERLEY.

1983. Rearing of twin pups to weaning by subantarctic fur seal *Arctocephalus tropicalis* female. S. Afr. J. Wildl. Res. 13:86-87.

CONDY, P. R.

1978. Distribution, abundance and annual cycle of fur seals (*Arctocephalus* spp.) on the Prince Edward Islands. S. Afr. J. Wildl. Res. 8:159-168.

1981. Annual food consumption, and seasonal fluctuations in biomass of seals at Marion Island. Mammalia 45:21-30.

CONDY, P. R., and M. N. BESTER.

1975. Notes on the tagging of seals at Marion and Gough Islands. S. Afr. J. Antarct. Res. 5:45-47.

CONDY, P. R., R. J. Van AARDE, and M. N. BESTER.

1978. The seasonal occurrence and behaviour of Killer Whales *Orcinus orca* (L.) at Marion Island. J. Zool. (Lond.) 184:449-464.

CONDY, P. R., and E. D. GREEN.

1980. The fur coat of the Amsterdam Island fur seal *Arctocephalus tropicalis*. J. Zool. (Lond.) 191:85-96.

De VILLIERS, A. F., and G. J. B. ROSS.

1976. Notes on numbers and distribution of fur seals, *Arctocephalus tropicalis* (Gray), on Marion and Prince Edward Islands, Southern Ocean. J. Mammal. 57:595-600.

KERLEY, G. I. H.

1981. A guide to the identification of fur seals on Marion Island. Cyclostyled internal rep., Mammal Res. Inst., Univ. Pretoria, Pretoria, 9 p.

1983a. Relative population sizes and trends, and hybridization of fur seals *Arctocephalus tropicalis* and *A. gazella* at the Prince Edward Islands, Southern Ocean. S. Afr. J. Zool. 18:388-392.

1983b. Comparison of seasonal haul-out patterns of fur seals *Arctocephalus tropicalis* and *A. gazella* on subantarctic Marion Island. S. Afr. J. Wildl. Res. 13:71-77.

1983c. Record for the Cape fur seal *Arctocephalus pusillus pusillus* from subantarctic Marion Island. S. Afr. J. Zool. 18:139-140.

1984. Relationships between sympatric breeding populations of fur seals (*Arctophalus* sp.) at the Prince Edward Islands. S. Afr. J. Sci. 80:28-29.

1985. Pup growth in the in fur seals *Arctocephalus tropicalis* and *A. gazella* on Marion Island. J. Zool. (Lond.) 205:315-324.

KERLEY, G. I. H., and M. N. BESTER.

1983. A note on whole mass corrections from piecemeal determinations for fur seals. S. Afr. J. Wildl. Res. 13:49-50.

MARSH, J. H.

1948. No pathway here. H. B. Timmins, Cape Town.

PAYNE, M. R.

1977. Growth of a fur seal population. Philos. Trans. R. Soc. Lond. B. 279:67-79.

RAND, R. W.

1956. Notes on the Marion Island fur seal. Proc. Zool. Soc. Lond. 126:65-82.

South African Fur Seal, *Arctocephalus pusillus pusillus*

JEREMY H. M. DAVID
Sea Fisheries Institute
Marine Mammal Laboratory
P.O. Box 251
Cape Town 5000
South Africa

HISTORY OF HARVESTING

Fur seal (*Arctocephalus pusillus pusillus*) harvesting is one of the oldest of all commercial fisheries in southern Africa (Muller 1942), although there are few early records of numbers taken. The first known sealers (Dutch) killed about 45,000 seals near the Cape of Good Hope in 1610 (Hart 1957; Shaughnessy 1984), and early Dutch sealing destroyed most of the colonies close to Cape Town. Before the arrival of Dutch settlers at Cape Town in 1652, French sealers were active on the islands in Saldanha Bay. Little further sealing occurred until the late 18th and early 19th centuries when British and American sealers were active on the west coast of southern Africa (Rand 1950a, 1972; Shaughnessy 1984).

There were no legal controls over the sealing industry until the Fish Protection Act of 1893, by which time over 20 island colonies had been extirpated. In the early days sealing was indiscriminate. Rookeries were invaded during the breeding season and all age groups including black pups were taken. As a result of the uncontrolled exploitation (for which there are no comprehensive catch statistics), the seal population was reduced to very low levels by the beginning of the 20th century. The 1893 Act stipulated that no seals be taken without a permit, but only in 1909 was a limit placed on the season. Sealing in South West Africa (Namibia) and its waters was controlled by the Sealing and Fisheries Proclamation in 1922, and by the Sealing and Fisheries Ordinance in 1949 (Shaughnessy 1984). This latter ordinance and the 1893 Act were repealed and replaced by the Sea Birds and Seals Protection Act in 1973, in which the Minister was empowered to prescribe the age, size, and sex of seals killed as well as the season and the localities where sealing would take place.

Harvesting has continued every year with few exceptions since 1900, and the details of the harvest since 1973 are shown in Table 1. The total known harvest of pups and bulls from 1900 to 1983 was over 2.5 million. Concessions to harvest were in force at 9 of the 23 breeding colonies up to June 1983. The average annual harvest was about 75,000 pups for the period 1973-82, but due to recent political developments in Europe and North America, the future of the sealing industry appears bleak.

POPULATION SIZE AND TRENDS

The South African fur seal, the only indigenous pinniped, breeds at 23 colonies around the coasts of South and South West Africa (Namibia), of which 6 are situated on the mainland, including the 4 largest, and 17 are on offshore islands. In addition there are at least another eight colonies where no breeding takes place and where numbers may fluctuate considerably. The population has grown dramatically since the turn of the century, and growth has been especially noticeable over the past 40 years. Regular censuses of black pups have been conducted only since 1971 (Table 2), and the rule of thumb devised for the northern fur seal, *Callorhinus ursinus* (Johnson 1972), namely to multiply the number of pups by 4, is used to calculate the total population size.

Since 1971 the population has shown a net annual growth rate of 3.7% despite continued exploitation. This growth, however, has been very unevenly distributed. Most of it has taken place at the 3 largest land colonies, whereas 13 of the 17 island colonies have declined. An interesting point is that the harvested colonies are increasing faster (mainland) or declining more slowly (island) than the unharvested colonies (Table 2). The approximate pup popula-

Table 1—Commercial harvest (annual pup catch) of South African fur seals in South Africa and Namibia, updating Appendix I of Best (1973).

Date	Seal I. Mossel Bay	Quoin Rock	Geyser Rock	Seal I. False Bay	Robbe-steen	Elephant Rock	Kleinsee	Sinclair I.	Albatross Rock	Long I.	Wolf & Atlas Bays	Luderitz I. (×4)	Hollam's Bird Is.	Cape Cross	Total Pups	Total Bulls
1900-1972															1,597,134[1]	120,393[1]
1973	2,150	1,421	2,310	2,839	458	449	15,582	454	224	1,543	45,891	—	—	7,353	80,674	2,246
1974	2,054	1,207	1,493	1,635	292	1,550	17,000	0	0	3,740	31,506	—	—	6,399	66,816	1,164
1975	1,638	970	138	139	350	872	13,615	4,222	1,668	5,282	35,616	744	—	9,543	74,945[2]	786
1976	—	806	—	—	365	1,097	5,318	4,294	1,125	3,831	30,968	1,689	1,879	11,095	62,467	0
1977	91[3]	323	482	—	171	—	14,000	5,117	1,567	4,189	35,823	—	—	14,631	76,394	1,099
1978	—	—	256	1,843	175	—	14,045	4,062	1,510	1,883	36,964	230	—	9,439	70,407	2,983
1979	—	—	—	2,656	—	—	15,000	4,288	1,503	3,861	38,628	—	—	9,147	75,083	387
1980	—	—	741	2,925	—	—	15,000	0	0	0	39,912	—	—	6,596	65,174	1,347
1981	—	—	0	1,069	—	—	20,043	4,020	1,693	5,012	42,136	—	—	12,992	86,965	640
1982	—	—	452	0	—	—	22,500	3,544	1,504	5,564	42,775	—	—	12,075	88,414	3,100
1983	—	—	0	0	—	—	0	0	0	0	40,580	—	—	2,139	46,739	4,020
Total															2,391,212	138,168

[1]Best (1973).
[2]+148 from Cape Frio.
[3]Illegal harvest.

Table 2—Estimates of pup production and population growth rate.

Colony	Pup population 1971 $\bar{x}$	Pup population 1971 SD	Pup population 1983 $\bar{x}$	Pup population 1983 SD	Annual growth (%) $\bar{x}$	Annual growth (%) SD
Cape Cross	15,797	3,429	22,596	4,251	3.12	2.54
Wolf Bay	16,849	4,405	29,481	3,908	5.01	2.61
Atlas Bay	28,497	4,980	66,604	11,174	7.36	2.31
Kleinsee	28,666	3,984	79,424	10,686	8.89	1.62
Van Reenen Bay	2,915	798	5,554	1,009	5.74	2.98
Lions Head	3,875	1,210	2,126	434	−4.60	2.81
Marshall Reef	1,045	339	120	48	−16.55	4.57
Staple Rock	3,614	1,314	1,495	529	−6.99	4.27
Boat Bay Rock	1,636	446	762	158	−6.01	3.06
Dumfudgeon Rock	2,343	587	540	90	−11.36	2.63
Long Islands	13,478	3,009	16,286	2,911	1.70	2.81
Albatross Rock	3,599	877	6,002	1,017	4.51	2.94
Sinclair Island	14,956	3,681	10,975	1,769	−2.35	2.95
Elephant Rock	1,354	272	2,269	553	4.35	3.30
Robbesteen	1,968	602	1,027	174	−5.02	2.72
Seal Island FB[1]	13,136	1,786	10,400	1,258	−1.90	1.46
Geyser Rock	3,530	737	8,216	1,163	7.42	2.31
Quoin Rock	3,164	688	653	166	−12.33	2.82
Seal Island MB[2]	3,297	603	528	117	−14.17	2.25
Hollam's Bird Islands	5,390	1,490	2,039	606	−7.73	3.49
Black Rock	163	88	326	63	7.02	4.92
Jacobs Reef	4,721	1,188	3,610	688	−2.07	2.75
Black Rocks AB[3]	1,037	307	328	81	−8.98	3.24
Mainland sealed	89,809	9,739	198,105	18,398	6.83	0.91
Mainland unsealed	6,791	1,519	7,680	1,188	1.16	2.12
Island sealed	67,122	7,716	59,272	4,880	−1.00	1.12
Island unsealed	11,311	2,073	6,303	996	−4.70	1.90
Mainland	96,600	10,337	205,785	18,905	6.52	0.88
Island	78,433	8,146	65,575	5,255	−1.46	0.99
North of Orange River	114,159	12,307	164,905	14,300	3.14	1.04
South of Orange River	60,874	5,012	106,455	11,516	4.75	0.98
All Colonies	175,033	15,095	271,360	20,334	3.73	0.66

[1]False Bay
[2]Mossel Bay
[3]Algoa Bay

tion size in 1983 was 271,000, indicating a total population of about 1.1 million animals.

Three methods are used for carrying out the census: (1) aerial photography between 17 and 22 December each year when the pups average about 3 weeks old; (2) tag-recapture in mid-January at selected colonies when the pups average about 6 weeks old; and (3) a second recapture sample obtained during the annual harvest from July to September at the same colonies. The biases associated with these three methods are believed to be as follows: (1) the aerial census is an underestimate due to the difficulties of counting black pups huddled in dense clumps or sheltering under rocks and in dark shadows; (2) tag-recapture is probably the most accurate, but is also likely to be an underestimate due to the tendency for pups to be clumped in the locations where they are marked and for sampling to take place in the same locations as a result of the difficulties of the very rugged terrain; and (3) the second recapture is probably an overestimate due to an apparent higher mortality of the tagged relative to untagged pups between initial marking and the harvest. A correction can be made by considering recaptures of male pups only which are hardier and suffer less mortality than the females. The best estimate of pup population size is considered to be the mean of the values from tag recapture and second recapture (2 and 3) (Shaughnessy in press).

INFLUENCES

Space

Arctocephalus pusillus pusillus is an animal of the shallow waters over the continental shelf. It is nonmigratory, but has been recorded at sea over 100 nmi from land (Rand 1956, 1967). Its colonies are distributed around 3,000 km of southern African coastline from Algoa Bay (lat. 34°S, long. 26°E) in the southeast to Cape Frio (lat. 18°30′S, long. 12°E) in the northwest. The general foraging area is usually within 50 nmi of the shore. As far as can be deduced from the usually low sighting frequency of seals at sea when over 10 mi from land during research cruises, it does not appear that there is any shortage of foraging space.

However, there is some evidence that suitable breeding sites may have been in short supply during this century. Traditionally the seals breed on small offshore islands which have an inherent limitation on space. None of the six mainland colonies, with the exception of Cape Cross, existed before about 1940. It seems likely, therefore, that as the population grew, the existing island colonies became inadequate and the seals spread from the islands to the adjacent mainland. (Four of the other five mainland colonies are opposite pre-existing island colonies.) It is also possible that excessive bull sealing, which occurred on these islands in the 1940's, caused significant disruption and precipitated movement of the seals to other less disturbed areas on the nearby mainland.

Since the four largest colonies are all situated on the mainland, it would appear that the absence of space restrictions is attractive to the seals. Furthermore, since five of the six mainland colonies are situated in restricted diamond areas, it would appear that man's influence in severely curtailing human interference, and in eliminating most large mammal predators, may have assisted in the establishment of these colonies. It is also interesting that none of the extinct island colonies destroyed by the early sealers had been permanently recolonized up to 1983. However, by 1985 there were definite signs that Mercury Island had re-established itself as a breeding colony.

Table 3—Total landings of marine organisms off South Africa and South West Africa from the Cunene River up to long. 30°E (excluding Natal).

Organism	Quantity (metric tons) 1972[a]	1981[b]
Pilchard (*Sardinops ocellatus*)	430,300	117,425
Anchovy (*Engraulis capensis*)	416,800	510,517
Mackerel (*Scomber japonicus*)	55,600	61,473
Horse mackerel (*Trachurus capensis*)	22,700	727,522
Other pelagic fish	37,600	39,712
Hakes (*Merluccius* spp.)	1,000,000	323,990
Other demersal fish	429,000	242,671
Line fish (incl. snoek)	25,000	29,794
Cephalopods	300	10,813
Rock lobster	7,600	6,916
Total	2,424,900	2,070,833

[a]Best 1973.
[b]ICSEAF 1981.

Food

By far the greatest part of the seal population (93%) breeds on the west coast due to the high productivity which occurs there. This in turn is supported by the cold northward-flowing Benguela current carrying nutrients and phytoplankton derived from Atlantic Central Water which upwells off the west coast. The South African fur seal is an opportunistic feeder and is known to prey on over 20 species of fish and cephalopods (Rand 1959; unpubl. data), of which about half are of commercial importance. Although there is perceived competition between seals and the commercial fisheries (about 57% of the total seal diet by weight is comprised of commercial species; unpubl. data), the seal population has continued to grow rapidly in the postwar era, coinciding with expansion of the fishing industry. The commercial catch of all marine organisms from the Cunene River to long. 30°E was 2.4 million tons in 1972 and declined by nearly 15% to under 2.1 million tons in 1981 (Table 3). This was due to a large drop in the quantity of demersal fish (including hake) and pilchard caught, but was compensated to some degree by a large increase in the amount of horse mackerel caught. Since the seal population has shown steady growth during this period, this seems to show not only that seals can cope with gross changes in the availability of specific prey species brought about by intensive fishing but also that carrying capacity of the west coast has not yet been reached, although continued growth of the fur seal population could change this situation sooner rather than later.

Competitors

Breeding sites—There is no competition with any other mammal for breeding sites. Although in historic times large colonies of breeding seabirds and seals did co-exist on the same islands (Shaughnessy 1984), today they are located almost exclusively on separate islands, with only small numbers of breeding seabirds to be found among the breeding seals. Interference by human encroachment may be significant on a few islands where guano is scraped regularly, and Robben Island in particular is permanently settled.

Food—Natural competitors for food in the Benguela system include other marine mammals, seabirds, and predatory fish. Among the former are four species of dolphins and an inshore stock of Bryde's

whales; the seabirds comprise primarily three species and the predatory fish, although there are at least eight species, comprise mainly two species. The food consumption of all these groups is unknown, but preliminary estimates indicate that annual consumption of anchovy by each group, south of lat. 31°S, is approximately as follows (Bergh et al. 1985): other marine mammals 21,000 tons; seabirds 50,000 tons; seals 75,000 tons; and predatory fish 520,000 tons. Commercial fisheries take over 500,000 tons of anchovy around the whole coast (Table 3). Comparison of recent results with those of Rand (1959) for the 1950's has shown a marked shift in the diet of the seals presumably brought about by commercial fishing (see Food section).

Predation

Little is known about predation on the South African fur seal. Its penchant for breeding on offshore islands eliminates the possibility of terrestrial predators in those localities. The mainland colonies, however, do not enjoy this protection, and the first-year pups are preyed on by black-backed jackals and brown hyenas (Shaughnessy 1979; pers. observ.).

At sea, known predators are sharks *Carcharodon* spp. and potential predators are killer whales *Orcinus orca* (Rand 1956; Shaughnessy 1982). Sharks are probably the most important of these since they are frequently seen in the vicinity of the rookeries. Seals showed limited regard for the underwater playback of killer whale sounds (Shaughnessy et al. 1981). Groups of seals responded initially by diving synchronously for 15-30 seconds, but soon resumed their former activities.

Survivorship

The only estimates of natural mortality rates available are preliminary estimates of pup mortality during the first 2 months of life, derived from aerial photographs taken at weekly intervals between November and mid-February at Seal Island, False Bay in 1974-75, and at Geyser Rock in 1981-82 and 1982-83. These suggest that mortality may be quite variable but could be as high as 20% between the time that maximum pup count was recorded (between 18 and 24 December) and 50 days later (unpubl. data).

In addition, collections of known-age material are being made routinely, and a reservoir of tagged animals of known age is being built up in the population. A sample of individually branded adults is also being monitored each breeding season at one breeding colony in Namibia (Van Reenen Bay).

REPRODUCTIVE PARAMETERS

First pupping

The proportion of a cohort that pups first at each age is not known. Rand (1955) believed that young cows mated at age 2 and produced the first pup at 3 years of age. The ages of his specimens were determined from an examination of skull sutures. We have not collected any data to support this contention. In August and September 1975 seven tagged females in their third year were killed at Kleinsee colony. None was pregnant, suggesting that first parturition does not occur until age 4 or later (Shaughnessy 1982). The only other data from known-age females concerns four tagged females killed at Kleinsee colony in 1979. They were all in their seventh year and were all pregnant. A reservoir of marked known-age animals in the population as well as age determination of the pelagic sample (see below) makes it possible to obtain more data on this topic.

Table 4—Analysis of pregnancy and size class of female South African fur seals collected at sea on five research cruises in August 1975, October 1977, August 1980, April 1981, and August 1982.

Standard length (cm)	No. females	No. pregnant	% pregnant
115-119	18	0	0
120-124	9	3	33.3
125-129	18	10	55.6
130-134	11	10	90.9
135-139	24	23	95.8
140-144	21	18	85.7
145-149	24	21	87.5
150-154	12	9	75.0
155-159	6	3	50.0
160-164	3	2	66.6
165-169	0		
170-174	1	1	100.0
Total (>120 cm)	129	100	77.5

Fecundity

Age-specific fecundity of adult females is not known. The pregnancy rate calculated by Best (1973) was 74%, based on data from 144 females collected at sea between 1954 and 1956 by Rand (1959). An analysis of the pregnancy rates of females collected at sea between 1975 and 1982 is presented in Table 4. Only females above 120 cm standard length were found to be pregnant, and for a sample of 129 females, the pregnancy rate was 77.5%. An analysis of age structure of this sample based on examination of sectioned canine teeth remains to be done.

Territorial status in males

Age of attainment of territorial status in males is unknown. Analysis of the age structure of a sample of 53 bulls collected on Seal Island, False Bay, during the breeding season may yield useful information.

REPRODUCTIVE ECOLOGY

Timing of pupping

Observations on this topic were made at Van Reenen Bay colony during at least part of every breeding season from 1977 through 1983. A small study area 21×12 m in extent was established in 1977, and the number of births occurring during 12-hour watches were recorded daily. The study area is set back about 40 m from the water's edge and is now only utilized during the breeding season. It is possible that the timing of the peak pupping date could differ slightly from that of cows pupping on the main beach area. Shaughnessy (1979) stated that 90% of births occurred in a 34-day period, but at Van Reenen Bay this period was only 26 days, from 22 November to 17 December (Fig. 1). The median pupping date

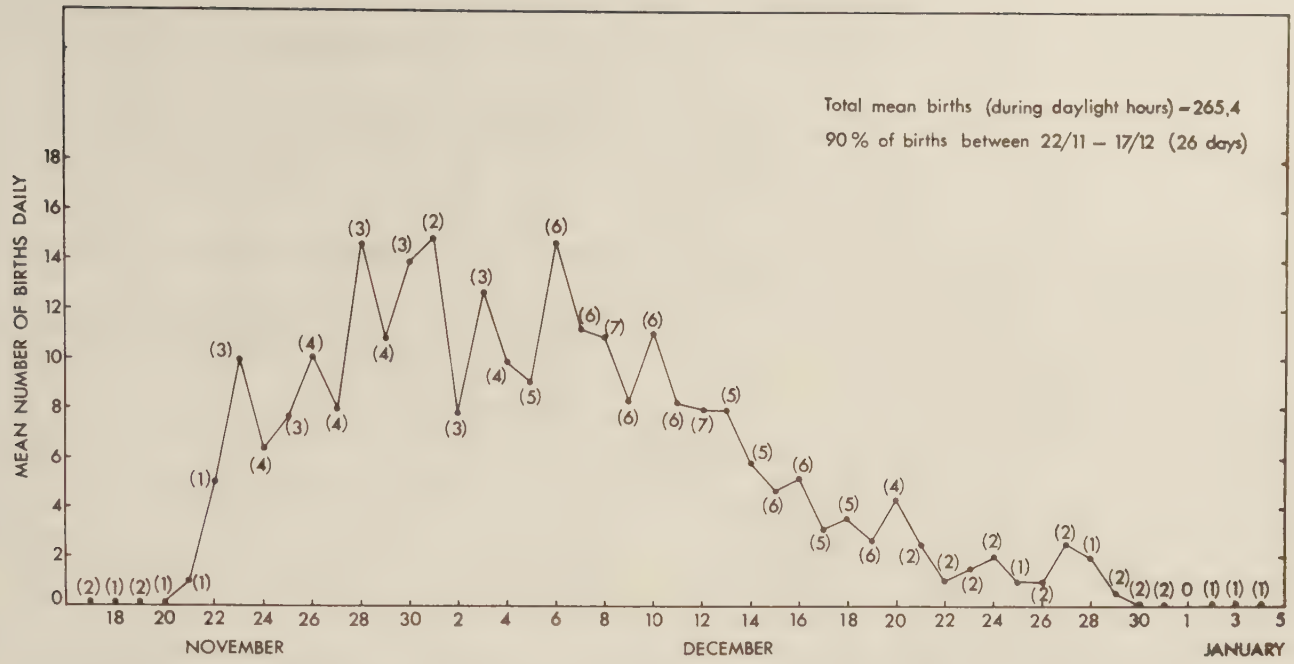

Total mean births (during daylight hours) = 265.4
90 % of births between 22/11 – 17/12 (26 days)
MEAN NUMBER OF BIRTHS DAILY
NOVEMBER
DECEMBER
JANUARY

Figure 1—Mean number of births daily at Van Reenen Bay, 1977-83, during watches 0600-1200h and 1300-1900h. Sample sizes in parenthesis (max. = 7). Median pupping date (when half total pups have been born) is December 4.

(when half the pups have been born) was 4 December. Shaughnessy and Best (1975) calculated the median pupping date on Seal Island, False Bay to be 1 December.

Density at peak breeding season

The maximum number of cows counted in the study area during the 1980 breeding season was 363 at 0800 h on 9 December (David and Rand 1986). Since the approximate area of the study site was 252 m^2, the peak density was 1.4 cows/m^2.

Gregariousness and group size

Since females are highly gregarious and it is normal for them to lie touching each other (with the exception of cows close to parturition and those with very young pups, which may be highly aggressive), the nearest neighbor distance is zero (Rand 1967; pers. observ.). Females do not associate in groups of specific size but form variable clumps with animals constantly joining or leaving throughout the day, so that numbers fluctuate continuously (Rand 1967). At the peak of the breeding season the main breeding beaches and rocks are packed with dense aggregations of cows, among which the only observable structure is conferred by the territories of the bulls.

Degree of polygyny

Rand (1967) calculated that at the north end of Seal Island, False Bay, in 1950 there were 135 harem bulls and 1,015 pups born, yielding a mean of 7.5 pups per bull. In the study area at Van Reenen Bay there was usually an average of about 10 territories during the peak of the season, with a relatively small number of bull replacements occurring (unpubl. data). Since total pup production in daylight hours was 265 (Fig. 1), this figure may be doubled to allow for births known to occur at night. Hence the mean number of births per territory was 53 over the whole season.

Attendance patterns of females

Lactation in the Cape fur seal is a lengthy process and may last for the whole period between one birth and the next (Rand 1950b, 1959). Weaning is a gradual process and quite variable in length. It may be completed by age 8 months (tagged pups have been harvested at a non-natal colony) but may last up to 18 months (Rand 1959) should the female happen to lose her new pup (second-year animals have been observed suckling; David and Rand 1986). Normally the pup is forcibly weaned on the birth of a new pup, if not independent already. Because of the long period of dependency, the cows make regular visits to the rookery during the nonbreeding season (January through October) for the purpose of feeding the pups.

No information is available on the total number of days spent ashore by cows between parturition and weaning. However, during the first 90 days postpartum, a mean of 41 days was spent ashore (N = 23 cows) at Sinclair Island in the 1948-49 breeding season and the mean visit duration was 2.4 days (N = 469; David and Rand 1986).

It is not known how many feeding trips to sea females make before weaning, but during the first 90 days postpartum, there was an average of five trips per month (N = 27 cows) with a mean duration of 2.9 days each (N = 444; David and Rand 1986).

GROWTH

The weight at birth is approximately 6 kg (Shaughnessy 1979). The complete growth for a year from birth (except the months of May and June) appears in Table 5. The tabulated weights are from two sources: (1) Rand's (1956) weights of live pups on Sinclair Island in 1949, and (2) weights of dead pups at harvests at various colonies since 1972. It is clear that the weights obtained by Rand are considerably higher than any mean weights obtained since that time. In particular, the weight of 35 kg obtained for males in August 1949

Table 5—Growth of South African fur seal pups from birth (November) to weaning (October).

	Mean monthly weight (kg)												
	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Source
Males	6	9.1	11.2	15.4	17.8	19.2	—	—	—	35.0	29.8	29.9	[a]
N	14	34	41	25	39	42				42	40	39	
Females	5.5	7.8	10.2	10.8	13.0	15.2	—	—	—	21.1	25.1	23.5	[a]
N	22	26	30	9	42	43				19	32	26	
Males									20.3	21.8	25.3	27.2	[b]
N									121	586	168	113	
Females									18.0	18.5	20.2	22.3	[b]
N									40	423	107	75	

[a]Rand (1956) live pups at Sinclair Island, 1949.
[b]Unpubl. data for dead pups at:

Cape Cross	1972 August, September, October
Sinclair Island	1978 August
Long Islands	1978 August
Cape Cross	1978 September
Atlas Bay	1979 August
Wolf Bay	1979 September
Cape Cross	1980 October
Kleinsee	1981 July
	1984 August

has not been verified at any harvest since then. In fact the mean weight for males in August since 1972 has been only 21.8 kg (Table 5). This could either reflect differences in equipment used or it could be a real difference indicating reduced food supplies for the females, presumably due to the impact on fish populations by commercial fishing operations which began in the 1950s.

The weaning weight can be approximated by obtaining the mean value of the August, September, and October data combined. For the 1972-84 data set this is 24.8 kg for males (N = 867) and 20.3 kg for females (N = 605).

The weights of adults are given as 700 kg for males and 122 kg for females in Shaughnessy (1979). However, these weights were given in pounds incorrectly published as kilograms. Rand (1956) states that the calculated maximum weight of bulls may reach 800 lb (353 kg). The heaviest actually weighed was 316 kg, and the mean weight of 53 bulls at Seal Island, False Bay, in the breeding season was 247 kg (unpubl. data). Old cows may weigh over 250 lb (114 kg; Rand 1956). However, the heaviest sexually mature female collected at sea weighed only 107 kg, and the next heaviest was 101 kg (N = 238). The mean weight of females collected at sea was 57.4 kg (N = 206; unpubl. data).

FOOD

The Cape fur seal is an opportunistic feeder and consumes both pelagic shoaling fish and demersal fish as well as cephalopods and small amounts of elasmobranchs and crustacea. Seabirds such as penguins and gannets may also be taken periodically (Cooper 1974; pers. observ.).

The contents of 245 stomachs collected during 1954-56 was, by volume, 67% fish, 21% cephalopods, 10% miscellaneous, and 2% crustaceans (Rand 1959). The most important fish species were horse mackerel, *Trachurus capensis*, and pilchard, *Sardinops ocellatus*, which comprised 39.7% and 12.9%, respectively, by volume, of total diet. Hake and anchovy each comprised 1.4% of total diet.

Another sample of stomachs was collected during three research cruises between Cape Town and the Orange River from 1980 to 1982. Seals were collected from 0.5 and 53 nmi from the coast. Undigested stomach contents were weighed and comprised 78.6% teleost fish, 19.6% cephalopods, 1.2% elasmobranch fish, and 0.5% crustaceans (N = 218). The fish portion of the diet consisted of about 74% demersal fish and 26% pelagic fish. The two most important species were found to be Cape hakes (*Merluccius capensis* and *M. paradoxus*) and anchovy (*Engraulis capensis*) which constituted about 32% and 14.8% of total diet, respectively, by weight. Pilchard and horse mackerel constituted only 0.5% and 0.2%, respectively, of the diet. The mean weights of the individual prey species were calculated from the sizes of otoliths collected from the stomachs. These are preliminary results and their adequacy as representative samples of the diet is unknown. An analysis of all stomach contents data collected between 1974 and 1985 is presented in David (1987).

ACKNOWLEDGMENTS

Thanks are due to P. B. Best for critical reading of the manuscript. Table 2 is derived from a computer simulation by D. S. Butterworth, University of Cape Town.

CITATIONS

BERGH, M. O., J. G. FIELD, and L. V. SHANNON.
1985. A preliminary carbon budget of the southern Benguela pelagic ecosystem. Int. Symp. Upw. W. Afr., Inst. Inv. Pesq., Barcelona, vol. 1:281-304.

BEST, P. B.
1973. Seals and sealing in South and South West Africa. S. Afr. Shipp. News Fish. Ind. Rev. 28:49-57.

COOPER, J.
1974. The predators of the jackass penguin, *Spheniscus demersus*. Bull. Br. Ornithol. Club 94:21-24.

DAVID, J. H. M.
1987. Diet of the South African (Cape) fur seal (1974-1985) and an assessment of competition with fisheries in southern Africa. *In* Payne, A. I. L., J. A. Gulland, and K. H. Brink (eds.), The Benguela and comparable ecosystems. S. Afr. J. Mar. Sci. 5.

DAVID, J. H. M., and R. W. RAND.
1986. Attendance behavior of South African fur seals. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur seals: Maternal strategies on land and at sea, p. 126-141. Princeton Univ. Press, Princeton.

HART, S.
1957. Der eerste Nederlandse tochten ter walvisvaart. Jaarb. van het Genootschap Amstelodamum, Amsterdam. 49:27-64.

ICSEAF.
1981. Statistical bulletin 11. Int. Comm. Southeast Atl. Fish., 92 p.

JOHNSON, A.
1972. Affidavit. *In* Ocean mammal protection hearings before the Subcommittee on Oceans and Atmosphere of the Committee on Commerce, United States Senate 92nd Congress, 2nd session, Part I. Wash., D.C., U.S. Gov. Print. Off., p. 783-787.

MULLER, C. J. F.
1942. Die geskiedenis van die visserye aan die Kaap tot aan die middel van die agtiende eeu. Argief-Jaarb. Suid Afr. Gesk. 5:1-100.

RAND, R. W.
1950a. The Cape fur seals. Farming in South Africa 25:305-307.
1950b. On the milk dentition of the Cape fur seal. Off. J. Dent. Assoc. S. Afr. 5:462-471.
1955. Reproduction in the female Cape fur seal, *Arctocephalus pusillus* (Schreber). Proc. Zool. Soc. Lond. 124:717-740.
1956. The Cape fur seal (*Arctocephalus pusillus*) (Schreber). Its general characteristics and moult. S. Afr. Div. Sea Fish. Invest. Rep. 21:1-52.
1959. The Cape fur seal (*Arctocephalus pusillus*). Distribution, abundance, and feeding habits off the south western coast of the Cape Province. S. Afr. Div. Sea Fish. Invest. Rep. 34:1-75.
1967. The Cape fur seal (*Arctocephalus pusillus*). 3. General behaviour on land and at sea. S. Afr. Div. Sea Fish. Invest. Rep. 60:1-39.
1972. The Cape fur seal (*Arctocephalus pusillus*). 4. Estimates of population size. S. Afr. Div. Sea Fish. Invest. Rep. 89:1-28.

SHAUGHNESSY, P. D.
1979. Cape (South African) fur seal. *In* Mammals in the Seas, p. 37-40. FAO Fish. Ser. 5, Vol. 2.
1982. The status of seals in South Africa and Namibia. *In* Mammals in the Seas, p. 383-410. FAO Fish. Ser. 5, Vol. 4.
1984. Historical population levels of seals and seabirds on islands off Southern Africa, with special reference to Seal Island, False Bay. S. Afr. Sea Fish. Inst. Invest. Rep. 127:1-61.
In press. Population size of the Cape fur seal *Arctocephalus pusillus*. II. From tagging and recapturing. S. Afr. Sea Fish. Inst. Invest. Rep.

SHAUGHNESSY, P. D., and P. B. BEST.
1975. The pupping season of the Cape fur seal, *Arctocephalus pusillus pusillus*. Unpubl. rep., Cape Town, Sea Fish. Res. Inst., 8 p.

SHAUGHNESSY, P. D., A. SEMMELINK, J. COOPER, and P. G. H. FROST.
1981. Attempts to develop acoustic methods of keeping Cape fur seals from fishing nets. Biol. Conserv. 21:141-158.

Australian Fur Seal, *Arctocephalus pusillus doriferus*

PETER D. SHAUGHNESSY
CSIRO Institute of Biological Resources
Box 225
Dickson, ACT 2602
Australia

ROBERT M. WARNEKE
Arthur Rylah Institute for Environmental Research
Box 137
Heidelberg, Victoria 3084
Australia

The Australian fur seal, *Arctocephalus pusillus doriferus* is found in southeastern Australian waters, primarily in Tasmania and Victoria, but also in southern New South Wales (Fig. 1). Its breeding range currently extends from lat. 32°38′S to lat. 43°52′S, with major breeding colonies located in Bass Strait between Victoria and Tasmania. The New Zealand fur seal *A. forsteri* also occurs in Australian waters. Its breeding range is west of that of *A. p. doriferus*, with colonies in South Australia and Western Australia.

Much of the following information on *A. p. doriferus* results from a long-term study carried out at Seal Rocks, Victoria, by Warneke. Recent accounts of this seal have been provided by Marlow and King (1974), Warneke (1982), and Warneke and Shaughnessy (1985).

HISTORY OF HARVESTING

Australian fur seals were subjected to a long period of commercial harvesting for skins and oil. This began in 1798, soon after the discovery of Bass Strait and its islands by Europeans. A partial reconstruction of the effects of the colonial sealing era in Australia to about 1825 can be made from records compiled by Cumpston (1963) of cargoes.

These records underestimate harvest figures, and those for the first 5 years seem especially low when one considers the sealing activity known to have occurred then. Some of this underestimation is because American vessels worked in Bass Strait without calling at Sydney, and at least one sealing merchant based in Sydney shipped skins to the Canton market with American sealers (Hainsworth 1972). Therefore, skins on these vessels are not included in the data portrayed in Figure 2.

Interpretation of Figure 2 is complicated by two important factors. First, three species of otariid seal initially occurred in Bass Strait: two fur seals, *A. p. doriferus* and *A. forsteri* (which were known as the brown and black fur seals, respectively), and the hair seal, *Neophoca cinerea* (Warneke 1982). Few cargo manifests of sealing vessels distinguished between skins of fur seals and hair seals; of those that did, none distinguished between the two species of fur seal. Second, some of the sealing voyages visited New Zealand as well as Australian waters, but did not itemize the seals taken from each locality.

The boom had passed by 1810, and most of the harvesting was over by 1825 when 300,000 or more skins had been taken from fur seal colonies in Australian waters. The proportion of *A. p. doriferus* is of course not possible to assess accurately. Based on the current abundance of the three species in southern and southeastern Australia (Warneke 1979; Crawley and Warneke 1979; King and Marlow 1979), the proportion could have been as high as two-thirds, indicating that about 200,000 *A. p. doriferus* may have been harvested in the period 1798 to 1825. It seems likely that the two least abundant species in Bass Strait (*A. forsteri* and *N. cinerea*) were eliminated during this early period of sealing. They have not recolonized Bass Strait, but still occur further west.

A second period of sealing followed, until the latter half of the nineteenth century. This was carried out by residents of the Bass Strait islands, the "straitsmen," who also harvested shearwaters, albatross, and wallabies (Murray 1927; Plomley 1966). This phase of sealing ceased when regulations to control seal harvesting were imposed, initially in Tasmanian waters (south of lat. 39°12′S) in 1889 under the Fisheries Act of 1889. Colonies in Victorian waters received legal protection in 1891 under the Game Act of 1890.

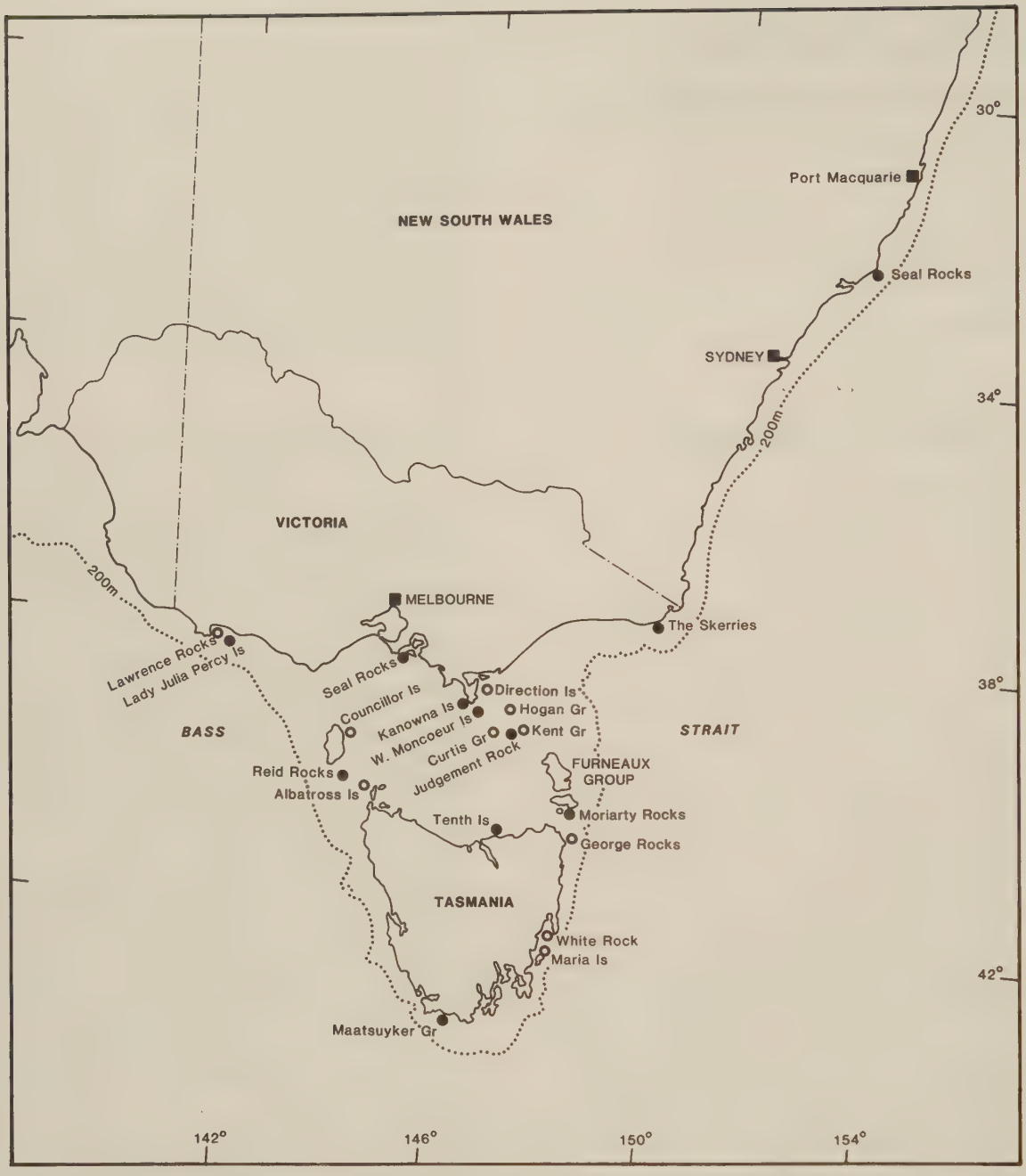


Figure 1—Map of southeastern Australia showing breeding range of the Australian fur seal *Arctocephalus pusillus doriferus* (from Warneke and Shaughnessy 1985). Closed circles represent breeding colonies; open circles denote former sites no longer used.

The Tasmanian regulations allowed sealing on a few islands in eastern Bass Strait by residents of Cape Barren Island on a regulated seasonal basis. Around 1923 the open season was changed from summer, when breeding colonies were readily accessible, to winter when weather conditions made access hazardous. The level of sealing then decreased even further.

Responsibility for seals in Tasmanian waters changed in 1975 from the Sea Fisheries Branch of the Department of Agriculture to the National Parks and Wildlife Service (Pearse 1979). Seals were then managed under the Wildlife Regulations of the National Parks and Wildlife Act of 1970. In Victorian waters, responsibility for conservation of fur seals is vested with the Department of Conservation, Forests and Lands under the Wildlife Act of 1975. No seal harvesting is allowed under both sets of legislation.

POPULATION SIZE AND TRENDS

Aerial surveys of most of the major fur seal sites of southeastern Australia were carried out in April 1945 and April 1975 (S. Fowler unpubl. data, CSIRO Archives; Pearse 1979). Both surveys occurred during cool, overcast weather when the majority of attendant seals was ashore. In addition, ground counts of sites in Victorian waters were made by Warneke between 1966 and 1982. As a result of these surveys and information concerning one colony in New South Wales, 11 breeding colonies and 21 nonbreeding sites are recognized (Fig. 1).

A comparison of counts made during the two aerial surveys indicates that there has been no substantial change in the status of

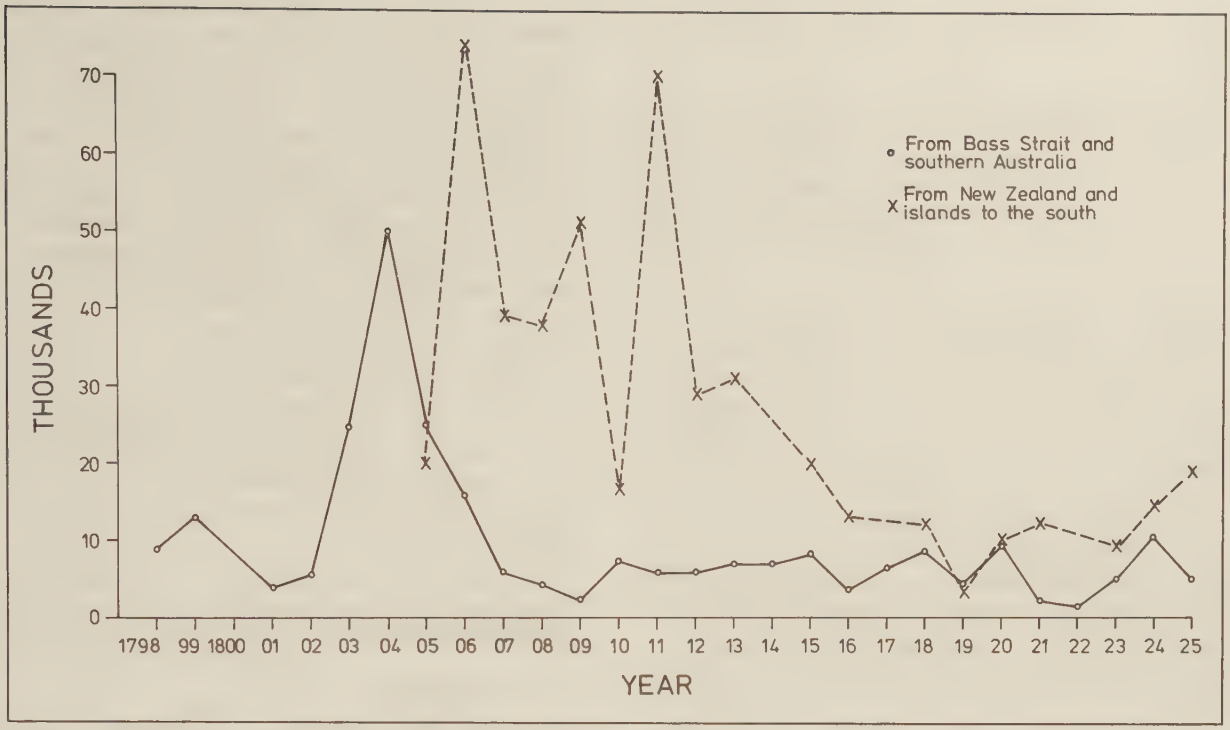

THOUSANDS
70
60
50
40
30
20
10
0
From Bass Strait and southern Australia
From New Zealand and islands to the south
1798 99 1800 01 02 03 04 05 06 07 08 09 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25
YEAR

Figure 2—Seal skins (*Arctocephalus* spp. and *Neophoca cinerea*) imported into Sydney from 1798 to 1825 (from Warneke and Shaughnessy 1985; based on Cumpston 1963).

A. p. doriferus between 1945 and 1975 (Warneke and Shaughnessy 1985). Further evidence of stability in the population level is provided by counts of pups at the Seal Rocks colony from 1966 to 1985. These have been about 2,000 annually (Warneke unpubl. data). From analyses of the survey data and by applying an index derived from comparisons of counts made at Seal Rocks during April and the breeding season of several years, Warneke and Shaughnessy (1985) estimated that 10,000 pups are born annually.

A complete survey of all breeding colonies of the Australian fur seal has never been made in one breeding season. Furthermore, the above comparison of the recent population level with that in 1945 is not ideal, because it is partly based on aerial surveys of sites made in the month of April, 4 months after the breeding season. By then adult numbers on the sites are well below maximum and may show large variation between successive days. Most estimates in the literature of levels of fur seal populations are based on pup numbers. The above comparison cannot be made on that basis as some pups have gone to sea by April, and most have molted and so are no longer recognizable as pups.

If a complete survey of colonies of the Australian fur seal were to be made, it is important that it take place during the breeding season and be directed at black pups, the only age class which is readily recognizable and which occurs simultaneously in all colonies. Such censusing should be repeated during several seasons so that fluctuations between years can be recognized.

Based on the current distribution of breeding colonies and non-breeding sites, evidence of additional sites occupied when commercial harvesting began (Warneke 1982), and also on the extent of the initial harvest between 1798 and 1825, Warneke estimates that the Australian fur seal population originally produced 20,000 to 50,000 pups annually (Warneke and Shaughnessy 1985). Thus the population is now much smaller than it was before European harvesting. Two factors that may have contributed to the maintenance of a low population level are: competition with fishermen for food in an ecosystem of low productivity, and an increase in mortality resulting from interactions with fishermen.

Space

Since the advent of commercial sealing in southeastern Australia, at least 4 sites, and possibly as many as 17, remain vacant (Fig. 1). One of these, Albatross Island in Bass Strait, was probably the largest breeding colony of *A. p. doriferus* (Warneke 1976). A few fur seals haul out there now, but no breeding is known to have occurred since the 1820s. Thus space (in the form of vacant sites) does not appear to be limiting expansion.

In territories of *A. p. doriferus* at Seal Rocks, Warneke determined that the density of cows averaged 0.15 m^2. For the Cape fur seal *A. p. pusillus*, Rand (1967) reported that the area of territories averaged 10 to 20 m^2 and contained 7 to 66 cows (mean 28). The density of cows in territories of *A. p. pusillus* therefore averaged 1.9 per m^2. Thus breeeding colonies of *A. p. doriferus* are less crowded than those of *A. p. pusillus*, and so space within colonies is not likely to be limiting expansion. This and strong philopatry presumably operate against recolonization of vacant sites.

Food

The marine habitat of the Australian fur seal is generally of low productivity. Bass Strait is dominated by warm, nutrient-poor water derived from the north and west, and is consequently of relatively low productivity. Productivity is higher off the south coast of New South Wales and the east coast of Tasmania, where upwelling occurs. These areas, however, are of limited significance because of their variability. As a result of this low marine productivity, the food resource of Australian fur seals is considered to be low and may well be limiting further expansion of numbers. However, this

does not explain why the fur seal population has not regained its original size.

A comparison of the productivity of the marine ecosystem of *A. p. doriferus* and that of *A. p. pusillus* indicates that the latter is much greater because of the high productivity of the Benguela Current on the west coast of southern Africa, where most of the Cape fur seals occur (Rand 1967; Warneke and Shaughnessy 1985). There is no counterpart to this current in Australian waters.

Competitors

Fishermen in Victorian waters claim that seals drastically reduce stocks of commercially valuable fish (Warneke 1982). That claim has not been substantiated by evidence from fishery statistics or from an examination of stomach contents and ejecta. But seals do interfere with sedentary mesh-net fisheries by damaging nets as well as mauling fish and allowing them to escape.

In Tasmanian waters seals occasionally interfere with fishing operations, but not sufficiently to cause conflict (Pearse 1979). A survey of line fishermen in 1980 by the National Parks and Wildlife Service of Tasmania indicated that 2% of their catch was damaged (Vivian 1982).

Some species of sharks, fish, seabirds, and dolphins compete with seals for prey, but to unknown extents.

Predators

Australian fur seals are preyed on by large sharks; the white pointer *Carcharodon carcharias*, in particular, preys on seals of all ages, although the extent of this mortality is unknown (Warneke 1982). The seals are also preyed on by humans; most of that mortality is inflicted by local fishermen. Analysis of tag returns indicates that a significant proportion of the mortality of immatures is caused by fishermen (Warneke 1975). Such mortality is either accidental, resulting from drowning in nets or traps, or deliberate when seals interfering with fishing operations are shot (Warneke and Shaughnessy 1985). Shooting by fishermen is authorized by permit (from Natl. Parks Wildl. Serv. and Dep. Conserv. Forests Lands) in Tasmanian and Victorian waters, respectively (Pearse 1979; Warneke pers. commun.).

Survivorship

Counts of dead pups in breeding areas at Seal Rocks reveal a minimum mortality rate of 15% in the first 2 months (Warneke 1982). During later stages of immaturity, many more seals die at sea. Analysis of an extensive array of tagging and resighting data accumulated over many years from the Seal Rocks colony by Warneke would enable survivorship of various age/sex classes to be estimated.

Resighting data of tagged seals indicate that longevity extends to at least 18 years in males and 21 years in females, and the latter are still capable of reproducing at 19 years (Warneke unpubl. data).

REPRODUCTION PARAMETERS

First pupping

Age at first oestrus is normally 4 years or later, although in a few females it occurs at 3 years of age (Warneke 1982).

Fecundity

Age-specific fecundity rates of adult females are not available, although analysis of relevant data collected from tagged animals at Seal Rocks by Warneke would enable these to be estimated. The overall pregnancy rate has been calculated as 68% (Warneke 1979) and 73% (Warneke and Shaughnessy 1985). The latter estimate follows from a reassessment of the animals included in the adult female class and from an increase in the sample size. Pregnant females and females heavier than the lightest pregnant female sampled were classified as adult.

Territorial status in males

Age of puberty in tagged males has been determined as 4-5 years. Attainment of breeding status does not occur until 8-13 years, with the average age of successful challengers for territories being 11 years. Males hold territories for an average of 1.8 years (Warneke and Shaughnessy 1985).

REPRODUCTIVE ECOLOGY

Timing of pupping

Pups are born from late October to late December at Seal Rocks, with a median date of 1 December (Warneke and Shaughnessy 1985). Ninety percent of pups are born in a 26-day period. It is not known if there are regional differences in pupping season.

Density within territories

Australian fur seals tolerate a high degree of bodily contact. The number of cows in breeding territories ranges from 0 to 63, with a mean of 9. Breeding territories range in size from 20 to 140 m^2, with a mean of 62 m^2 (Warneke and Shaughnessy 1985). Thus the mean density of cows in breeding territories is 0.15 per m^2, with range 0 to 3.1.

Degree of polygyny

The number of pups born on the main beach of Seal Rocks averaged 10 per territory in an area with 95 to 100 bulls (Warneke unpubl. data).

Attendance patterns of females

Cows are ashore with their pups during the 6-day period between birth and oestrus. Soon after mating they feed at sea for a few days before returning to suckle their pups. After the first trip to sea, periods at sea increase to about a week, alternating with several days ashore. Analysis of Warneke's data on sighting of tagged cows at Seal Rocks may provide more precise estimates of these parameters.

The lactation period lasts about 11-12 months, although pups are believed to begin foraging by age 7 months. There is considerable variation between individuals in the timing and causes of weaning. Some juveniles continue nursing into their second and, less commonly, their third years (Stirling and Warneke 1971). Counts of young seals in association with cows have been made in several seasons during late November and early December (when most pups have been born). Eleven percent of them were older than 1 year (Warneke unpubl. data).

GROWTH

Body mass (kg) of about 20 newborn pups of each sex in November is:

males	$\bar{x}$	8.1	(range 5.0-12.5)
females	$\bar{x}$	7.1	(range 4.5-10.0).

In January, about 1 month after birth, the body mass data (kg) are:

males	$\bar{x}$	12.0	(range 7.0-18, n = 337)
females	$\bar{x}$	10.0	(range 5.0-14, n = 198).

Body mass at weaning is highly variable as a result of variation in the timing and causes of weaning.

Body mass data (kg) for adults are:

males	$\bar{x}$	279	(range 218-360, n = 13)
females	$\bar{x}$	76	(range 41-113, n = 71).

Data for newborn pups are from Warneke (1979); those for month-old pups and adults are from Warneke and Shaughnessy (1985). Adult males were all territorial bulls; adult females are defined above. The data for adult females differ slightly from that in Warneke (1979) and is more accurate.

FOOD

Food items have been studied by Lewis (1930), Tubb and Brazenor (1937), and McNally and Lynch (1954). Numbers of stomachs with food items examined by these investigators were 18, 1, and 138, respectively. For each series, seals were killed either at the breeding colonies of Seal Rocks or Lady Julia Percy Island in Victoria, or in nearby waters. In addition, Warneke (1982; unpubl. data) has made observations on feeding, stomach contents (very few), and vomit. The most important prey are fish, cephalopods, and crustaceans. In general the Australian fur seal is an opportunistic feeder.

A wide range of fish is taken, depending on seasonal availability and local opportunity. They include surface, midwater, and bottom-dwelling species, at least 20 of which have been identified. The most important is snook, *Leionura atun*, which often occurs in large shoals in Bass Strait in summer. The most frequently taken cephalopods are squid (*Nototodarus* and *Sepioteuthis*), cuttlefish (*Sepia*), and octopus (*Octopus*). Of crustaceans, rock lobster (*Jasus*) are taken occasionally and crabs have been found in stomachs of starveling juveniles.

A comparison of prey items in the diet of *A. p. pusillus* of southern Africa and *A. p. doriferus* revealed many similarities at the generic level and several at the species level (Warneke and Shaughnessy 1985).

Evidence from recoveries of seals drowned in rock lobster traps, fish traps, and deep-seal trawls indicates that the Australian fur seal dives to a depth of at least 100 m (Warneke unpubl. data). Recoveries from trawl nets at greater depths indicate that some animals dive to 200 m. This suggests that the whole of the continental shelf is available as a feeding area. In addition, there is evidence that adults search the deeper waters off the shelf edge (Warneke 1982).

Captive females of average size (about 75 kg) require approximately 5 kg of food per day to maintain their body mass, or about 7% of their body mass (Warneke 1979). No other quantitative data are available on the food requirements of Australian fur seals.

CITATIONS

CRAWLEY, M. C., and R. WARNEKE.
1979. New Zealand fur seal. *In* Mammals in the seas, p. 45-48. FAO Fish. Ser. 5, Vol. 2.

CUMPSTON, J. S.
1963. Shipping arrivals and departures Sydney, 1788-1825. Published by author, Sydney, 190 p.

HAINSWORTH, D. R.
1972. The Sydney traders. Simeon Lord and his contemporaries 1788-1821. Cassell, Melbourne, 264 p.

KING, J. B. (sic), and B. J. MARLOW.
1979. Australian sea lion. *In* Mammals in the seas, p. 13-15. FAO Fish. Ser. 5, Vol. 2.

LEWIS, F.
1930. Seals on the Victorian coast and their feeding habits. Aust. Mus. Mag. 4:39-44.

McNALLY, J., and D. D. LYNCH.
1954. Notes on the food of Victorian seals. Unpubl. fauna rep. 1:1-16. Off., Dir. Fish. Game, Victoria.

MARLOW, B. J., and J. E. KING.
1974. Sea lions and fur seals of Australia and New Zealand - the growth of knowledge. Aust. Mammal. 1:117-135.

MURRAY, L. C.
1927. An account of the whaling and sealing industries of Van Diemen's Land. B.A. Thesis. Univ. Tasmania, 42 p.

PEARSE, R. J.
1979. Distribution and conservation of the Australian fur seal in Tasmania. Victorian Nat. 96:48-53.

PLOMLEY, J. B.
1966. Friendly mission. The Tasmanian journals and papers of George Augustus Robinson 1829-1834. Tasmanian Historical Res. Assoc., Hobart, 1074 p.

RAND, R. W.
1969. The Cape fur-seal (*Arctocephalus pusillus*). 3. General behaviour on land and at sea. S. Afr. Div. Sea Fish. Invest. Rep. 60:1-39.

STIRLING, I., and R. M. WARNEKE.
1971. Implications of a comparison of the airborne vocalizations and some aspects of the behaviour of the two Australian fur seals, *Arctocephalus* spp., on the evolution and present taxonomy of the genus. Aust. J. Zool. 19:227-241.

TUBB, J. A., and C. W. BRAZENOR.
1937. Mammalia. *In* Lady Julia Percy Island. Report of the expedition of the McCoy Society for field-investigation and research. Proc. R. Soc. Victoria 49:435-437.

VIVIAN, H.
1982. Natural history and status of the Australian fur seal, *Arctocephalus pusillus doriferus* in Tasmanian waters. Environ. Stud. Rep. 1982/1, Univ. Tasmania, 55 p.

WARNEKE, R. M.
1975. Dispersal and mortality of juvenile fur seals *Arctocephalus pusillus doriferus* in Bass Strait, southeastern Australia. Rapp. P-v. Reun. Cons. int. Explor. Mer 169:296-302.
1976. Preliminary report on the distribution and abundance of seals in the Australasian region. Rep. ACMRR/MM/SC/42, Cons. Marine Mamm., Bergen, Norway, 46 p.
1979. Australian fur seal. *In* Mammals in the seas, p. 41-44. FAO Fish. Ser. 5, Vol. 2.
1982. The distribution and abundance of seals in the Australasian region, with summaries of biology and current research. *In* Mammals in the seas, p. 431-475. FAO Fish. Ser. 5, Vol. 4.

WARNEKE, R. M., and P. D. SHAUGHNESSY.
1985. *Arctocephalus pusillus*, the South African and Australian fur seal: taxonomy, evolution, biogeography, and life history. *In* Ling, J. K., and M. M. Bryden (eds.), Studies of sea mammals in south latitudes, p. 53-77. South Aust. Mus., Adelaide.

Subantarctic Fur Seal, *Arctocephalus tropicalis*, in French Subantarctic Territories

JEAN-PAUL ROUX[1]
Institut des Sciences de l'Evolution
Section Socioecologie
U.S.T.L. Place Bataillon
34060 Montpellier Cedex
France

INTRODUCTION

The Subantarctic fur seal *Arctocephalus tropicalis* breeds on two groups of French islands in the southern Indian Ocean: the Crozet group (lat. 46°S, long. 51°E) and Saint Paul (lat. 38°43′S, long. 77°30′E) and Amsterdam Islands (lat. 37°50′S, long. 77°35′E). As in other localities (Prince Edward and Gough Islands), these local seal populations are recovering from uncontrolled harvesting operations. On the Crozet Islands, the recently discovered breeding colony comprises the two species *A. tropicalis* and *A. gazella* (Jouventin et al. 1982), the latter much smaller in numbers than the first. Some historical accounts seem to prove that prior to exploitation *A. gazella* was the only fur seal present on the Crozet Islands (Roux, unpubl. data).

HISTORY OF HARVESTING

Fur seals were extremely abundant on Saint Paul and Amsterdam Islands, according to early visitors, until the end of the 18th century (Valentyn 1726; Staunton 1797; Claret de Fleurieu 1799; La Billardiere 1801; de Rossel 1808; Peron 1824). Seals were perhaps taken as early as the first landings on these islands in 1696 or 1734. The first recorded sealing expedition in 1789 took 1,200 skins in 9 days (Allen 1899). Between 1789 and 1832, at least 22 sealing vessels plus numerous whalers were engaged in regular and intensive harvesting on both islands (Staunton 1797; Peron 1824; Goodridge 1841; Allen 1899; Stackpole 1953; de Brossard 1971). From 1837 to the end of the century, these islands were visited each year by fishermen, whalers, and occasionally sealers. Fur seals appeared to have stopped breeding on Saint Paul Island after 1835. In 1850 they were still breeding in extremely reduced numbers on Amsterdam Island, and continued to be exploited until 1874 and probably 1876 (de Ravisi 1853; Von Pelzeln 1861; Velain 1877; Velain 1878). By the beginning of the 20th century, fur seals were believed to be extinct on both islands (Vanhoffen 1909; Aubert de la Rue 1932; Jeannel 1940), until 1950 when a breeding colony was found on the northwest sector of Amsterdam Island (Martin de Vivies 1951; Paulian 1953).

Harvesting had started by 1803 in the Crozet group (Fanning 1834; Stackpole 1953) with regular and intensive sealing activity from 1814 to 1850 (Allen 1899; Aubert de la Rue 1953; Derenne et al. 1976). Authors stated that fur seals were already not so numerous by 1820-25 (Lesquin 1827; Goodridge 1841). They had almost disappeared by 1887, when a sealing party took only three skins in a 5-month campaign (Allen 1899). Sealers continued their campaigns on these islands for elephant seal oil until 1928 (Aubert de la Rue 1953, 1954; de Brossard 1971).

For both groups of islands, harvesting was totally uncontrolled and nonselective. It is probable that fur seals were exterminated on Saint Paul Island and the Crozet group by the end of the 19th century but that some seals remained on the west coast of Amsterdam Island.

POPULATION SIZE AND TRENDS

Census methods and population size

A complete census was made during the 1981-82 breeding season on Amsterdam Island. Correction factors were applied to allow for

[1]Present address: Sea-Fisheries, P.O. Box 394, 9000 Lüderitz, S.W.A./Namibia.

pup mortality, adult female pregnancy rate, and using summer haulout data for adult males. Yearlings, absent from the island during the breeding season, were not included in the estimates (Hes and Roux 1983).

The Amsterdam Island fur seal population, excluding yearlings, totaled over 35,000 individuals in 1982 (Roux 1982; Hes and Roux 1983: 6,070 adult males; 12,972 adult females; 5,085 subadults, and 10,898 pups).

On Saint Paul Island, no complete census has been made since 1971 (Segonzac 1972); partial counts were made in 1981 (G. Cesa pers. commun.), 1983 (B. Tollu unpubl. data), and 1985 when a pup census was carried out.

The present size of the Saint Paul Island subpopulation is unknown, but a large increase has occurred since 1971 when it totaled about 350 individuals (Segonzac 1972). During a short visit to this island in December 1984, the author counted 1,362 fur seals (mainly subadults) on 26% of the coastline. A census in February 1985 disclosed 66 pups born on this island during the 1984-85 breeding season (Roux unpubl. data).

Complete counts have been made annually for the Crozet islands since 1978. They have taken place on Possession Island during the breeding season. No correction factors are applied here, as data on pup mortality and adult female pregnancy rate are not available.

On Crozet Islands, the total population in 1984 was about 350 individuals, including 100 pups at the breeding colony of Possession Island (P. Frigola pers. commun.). Isolated births are known to occur regularly on East and Hog Islands (Jouventin et al. 1982; Voisin 1984; H. Weimerskirch pers. commun.).

Trends

Between 1970 and 1982 the mean annual rate of increase on Amsterdam Island was 16.4% for total numbers and 16.6% for numbers of pups (Hes and Roux 1983).

On Saint Paul Island the estimated annual rate of increase was over 17.4% for total numbers between 1970 and 1981. From 1971 to 1985 the number of pups born increased at a mean annual rate of 16.0%.

The mean annual rate of increase on the Crozet Islands from 1979 to 1984 was 16.2% for total numbers (Jouventin et al. 1982; unpubl. data). From 1978 to 1985 the number of pups born increased at an average annual rate of 18.2% (Fig. 1).

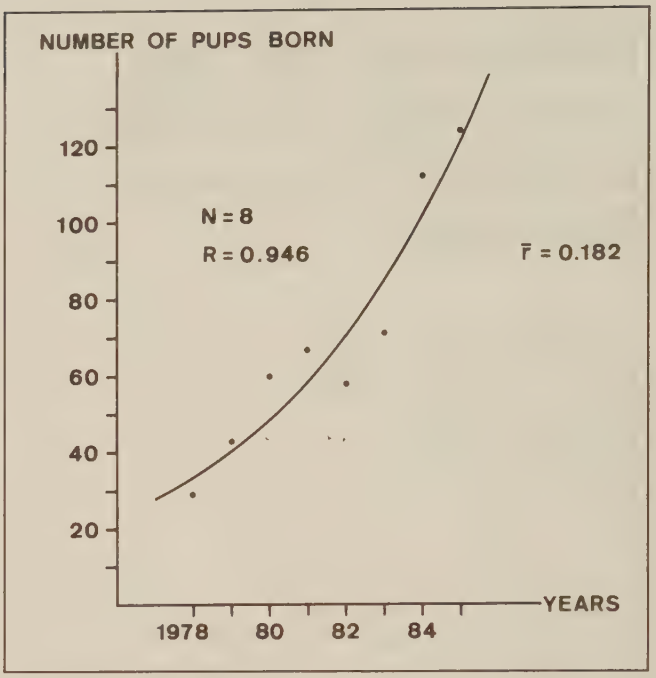


Figure 1—Evolution of the Possession Island breeding colony (Crozet group).

SURVIVORSHIP

Pup mortality

At the study colony on Amsterdam Island, mortality of pups up to 6 weeks of age was 13.5% and about 15.0% up to 12 weeks of age in 1982 (Hes and Roux 1983). On this island, pup mortality rates are known to vary greatly with density and beach characteristics such as morphology, topography, and orientation.

REPRODUCTIVE PARAMETERS

Pregnancy rate and sex ratio

An estimated pregnancy rate was calculated for the Amsterdam Island population by dividing the number of pups born at the study colony by the cumulative number of adult females hauling out during the pupping period. This gave a rate of 84% in 1982 (Hes and Roux 1983).

The sex ratio (R) of the pups at the age of 2 months is close to unity (R=1.131, N=976, χ^2=3.688, $0.10<p<0.05$), as it is at 10 months of age (R=1.299, N=200, χ^2=3.38, $0.10<p<0.05$) during weaning (Roux unpubl. data).

REPRODUCTIVE ECOLOGY

Timing and duration of the pupping period and distribution of births

On Amsterdam Island pupping occurs over a period of 39 days (24 November to 1 January). The median date of birth, calculated from a simplified probit analysis (Caughley 1977), was 11 December in 1981 (Roux and Hes 1984); 90% of births occurred within a period of 29 days (30 November to 28 December, Roux unpubl. data).

Density at peak during the breeding season

A density index was calculated for Amsterdam Island using the number of animals per unit of coastline length. The highest densities observed in 1981-82 were 1,255 and 1,229 births per 570-m coastal segment. Density varies directly with the time elapsed since the colonies were founded (Roux 1987).

Degree of polygyny

The degree of polygyny varies according to density and beach topography. About 1.5 pups per territorial male are born on a medium density rocky beach, 5.5 pups on a high density boulder beach on Amsterdam Island, and approximately 3.0 pups on the Crozet breeding colony.

Lactation period

Weaning occurs in October on Amsterdam Island; the latest observed date in 1981 was 25 October. The median date of weaning was 15 October; thus the lactation period lasted 10 months (calculated from the median date of birth) to 11 months (calculated from the first birth date) (Roux and Hes 1984).

Growth

On Amsterdam Island the birth weight is 4.9 kg (N=25, range 3.6-6.1) for males and 4.0 kg (N=29, range 3.3-4.5) for females (Paulian 1964). At weaning (310 days old), males weighed 18.15 kg (N=55, SD=2.29) and females weighed 15.45 kg (N=46, SD=2.47) in October 1981 (Roux unpubl. data).

The four males aged 6 years and older which were studied by Paulian (1964) weighed 121.0 kg (N=4, SD=35.0, range 91-164), and the two females aged 2 years and older weighed 40 kg and 56 kg, respectively.

Food

On Amsterdam Island *A. tropicalis* is known to prey upon squid, fish, and rockhopper penguins (Paulian 1964; B. Tollu unpubl. data; Roux unpubl. data). Otoliths and squid beaks have been collected from scats and vomit, but have not yet been identified.

CITATIONS

ALLEN, J. A.
1899. Fur seal hunting in the Southern hemisphere. *In* Jordan, D. S. (ed.), The fur seals and fur-seal islands of the North Pacific, Part 3, p. 307-321. U.S. Treas. Dep., Wash., D.C., 1898-99.

AUBERT de la RUE, E.
1932. La faune des îles Saint Paul et Amsterdam. Terre Vie 2:642-662.
1953. Les Terres Australes. Que sais je? 603. Presses Universitaires de France, 127 p.
1954. Deux ans aux îles de la Désolation, Archipel de Kerguelen. Science et Voyages, Julliard R., Paris, 316 p.

de BROSSARD, M.
1971. Kerguelen, le découvreur et ses îles. 2, îles Australes. France Empire, Paris, 541 p.

CAUGHLEY, G.
1977. Analysis of vertebrate populations. John Wiley, New York, 234 p.

CLARET de FLEURIEU, C. P.
1799. Voyage autour du monde pendant les années 1790, 1791 et 1792 par Etienne Marchand. Imprimerie de la Republique, Paris.

DERENNE, P., J-L. MOUGIN, C. STEINBERG, and J-F. VOISIN.
1976. Les oiseaux de l'île aux Cochons, archipel Crozet (46°06′S, 50°14′E). CNFRA (Comn. Natl. Fr. Rech. Antarct.) 40:107-148.

FANNING, E.
1834. Voyages around the world with selected sketches of voyages to the south seas. O. Rich, New York, 499 p.

GOODRIDGE, C. M.
1841. Narrative of a voyage to the south seas and the shipwreck of the Princess of Wales cutter... Featherstone, Exeter, 170 p.

HES, A. D., and J-P. ROUX.
1983. Population increase in the subantarctic fur seal *Arctocephalus tropicalis* at Amsterdam Island. S. Afr. J. Antarct. Res. 13:29-34.

JEANNEL, R.
1940. Au Seuil de l'Antarctique. Publ. Mus. Natl. Hist. Nat., Paris N°5, 236 p.

JOUVENTIN, P., J-C. STAHL, and H. WEIMERSKIRCH.
1982. La recolonisation des îles Crozet par les otaries (*Arctocephalus tropicalis* et *A. gazella*). Mammalia 46:505-514.

La BILLARDIERE, J. J.
1801. Relation du voyage a la recherche de La Perouse... H. J. Jansen, Paris.

LESQUIN, W.
1827. Relation du naufrage de la goelette l'Aventure, de l'île de France commandée par M. Lesquin de Roscoff. Extrait du Lycée Armoricain, Mellinet-Malassis, Nantes, 52 p.

MARTIN de VIVIES, P.
1951. Mission a l'île Amsterdam, rapport préliminaire. Unpubl. rep., Terres Australes et Antarctiques Francaises, Paris.

PAULIAN, P.
1953. Pinnipèdes, cétacés et oiseaux des Iles Kerguelen et Amsterdam. Mem. Inst. Res. Sci. Madagascar, Ser. A 8:111-234.
1964. Contribution à l'étude de l'otarie de l'île Amsterdam. Mammalia 28:3-146.

PERON, P.
1824. Mémoires du capitaine Peron sur ses voyages en Afrique, en Arabie... Brissot-Thivars, Paris.

de RAVISI, T.
1853. Les îles Saint Paul et Amsterdam. Jamin, Saint-Denis, Ile de la Réunion, 131 p.

de ROSSEL, E. P.
1808. Voyage de d'Entrecasteaux envoyé à la recherche de La Perouse. Imprimerie Imperiale, Paris, 1:40-46.

ROUX, J-P.
1982. L'otarie d'Amsterdam. Actes VIeme Colloq. Mammal., La Rochelle, p. 75-79.
1987. Recolonization processes in the subantarctic fur seal, *Arctocephalus tropicalis*, on Amsterdam Island, p. 189-194. *In* Croxall, J. P., and R. L. Gentry (eds.), Status, biology, and ecology of fur seals. U.S. Dep. Commer., NOAA Tech. Rep. 51.

ROUX, J-P., and A. D. HES.
1984. The seasonal haul-out cycle of the fur seal *Arctocephalus tropicalis* (Gray, 1872) on Amsterdam Island. Mammalia 48:377-389.

SEGONZAC, M.
1972. Données récentes sur la faune des îles Saint Paul et Nouvelle Amsterdam. Oiseau Rev. Fr. Ornithol. 42:3-68.

STACKPOLE, E. A.
1953. The sea hunters, the New England whalemen during two centuries: 1635-1835. J. B. Lippincott, New York, 510 p.

STAUNTON, G.
1797. an authentic account of an Embassy from the King of Great Britain to the Emperor of China... G. Nicol, London.

VALENTYN, F.
1726. Oud en Nieuw Oost Indien... vol. 4. p. 68-71, Amsterdam.

VANHOFFEN, E.
1909. Tiere und Pflanzen von St-Paul und Neu amsterdam. Deutche Sud Polar Exped. 2:399-410.

VELAIN, C.
1877. Passage de Vénus sur le Soleil. Expédition Francaise aux îles Saint Paul et Amsterdam: Zoologie. Observations générales sur la faune des deux îles suivies d'une description des mollusques. Arch. Zool. Exp. Gen. 6:1-144.
1878. La faune des îles Saint Paul et Amsterdam et description géologique de la presqu'île d'Aden, de l'île de la Reunion, des îles Saint Paul et Amsterdam. Rev. Sci. II, 14:1222-1230.

VOISIN, J-F.
1984. Observations on the birds and mammals of ile aux Cochons, Crozet Islands, in February 1982. S. Afr. J. Antarct. Res. 14:11-17.

Von PELZELN, A.
1861. Reise der Osterreichishen fregatte "Novara" um die Erde in den Jahren 1857, 1858, 1859. Zool. T1:227-273 (Wien).

Breeding Behavior of the Guadalupe Fur Seal, *Arctocephalus townsendi*

MARK O. PIERSON
Institute for Marine Studies
University of California
Santa Cruz, California 95064

INTRODUCTION

The Guadalupe fur seal, *Arctocephalus townsendi*, is the only representative of its genus in the northern hemisphere. Like the other species of *Arctocephalus*, its numbers were severely reduced by commercial hunting in the nineteenth century, and for many years it was considered extinct (Hubbs 1956). At present, the species breeds only on Isla de Guadalupe off the coast of Baja California, Mexico. The population is still quite small, perhaps numbering as few as 2,000 animals, but apparently is growing; Fleischer (1978, 1987) estimated the growth rate between 1954 and 1977 to have been approximately 10% per year.

Although the Guadalupe fur seal has been censused fairly regularly since its rediscovery in 1954, little research has been done on other aspects of the species' biology (Peterson et al. 1968). Previous to this work, only one week-long study had been made of the breeding behavior of this species (Peterson and Ramsey 1970). This paper reports the results of a season-long field study of the breeding behavior of *A. townsendi* that focused on the territorial behavior of adult males. Data were also collected on other aspects of the behavior of this little-known species.

METHODS

Isla de Guadalupe is an oceanic island of volcanic origin, located 260 km west of Baja California, Mexico (Fig. 1). The island is bathed by the cold waters of the California Current, and prevailing winds are from the northwest. Most of the shoreline on the leeward east side of the island, the area occupied by the fur seals, is composed of jumbled basaltic rocks and boulders bounded by towering cliffs and containing numerous crevices and caves of various sizes. By 1977, fur seals bred along roughly 25 km of this shoreline, from Discovery Point in the north to Melpomene Cave in the south (Fig. 1).

The study was carried out in two parts. The first, more extensive phase was conducted on Isla de Guadalupe from 12 June to 12 July 1975. A total of 265 hours was spent in observation at the main study area, an open stretch of rocky shoreline approximately 120 m long that contained four small coves divided by lava dikes and a wide, flat point. The territories of eight adult males were in this study area (Fig. 2). This area was located approximately halfway down the east side of the island, immediately north of the Lobster Camp cove. Additional observations were made at the cove itself, which sheltered three or four territories and 20 to 60 juvenile fur seals. Another site for behavioral observations was a large cave (about 50 m wide by 40 m deep), which had previously been used as a study area by Peterson and Ramsey (1970).

Additional observations were made between 23 June and 10 July 1977, in the course of a fur seal survey of Isla de Guadalupe (Fleischer 1978). In particular, observations were conducted at the 1975 main study area on 7-8 July, and at a large open cave near Punta Proa on 9 July (Fig. 1).

RESULTS

Male territorial behavior

Timing—When observations began on 12 June 1975, seven of eight males in the main study area were already established on territories, and adult males occupied nearly all the suitable terrain along the shoreline within 2 km of the study area.

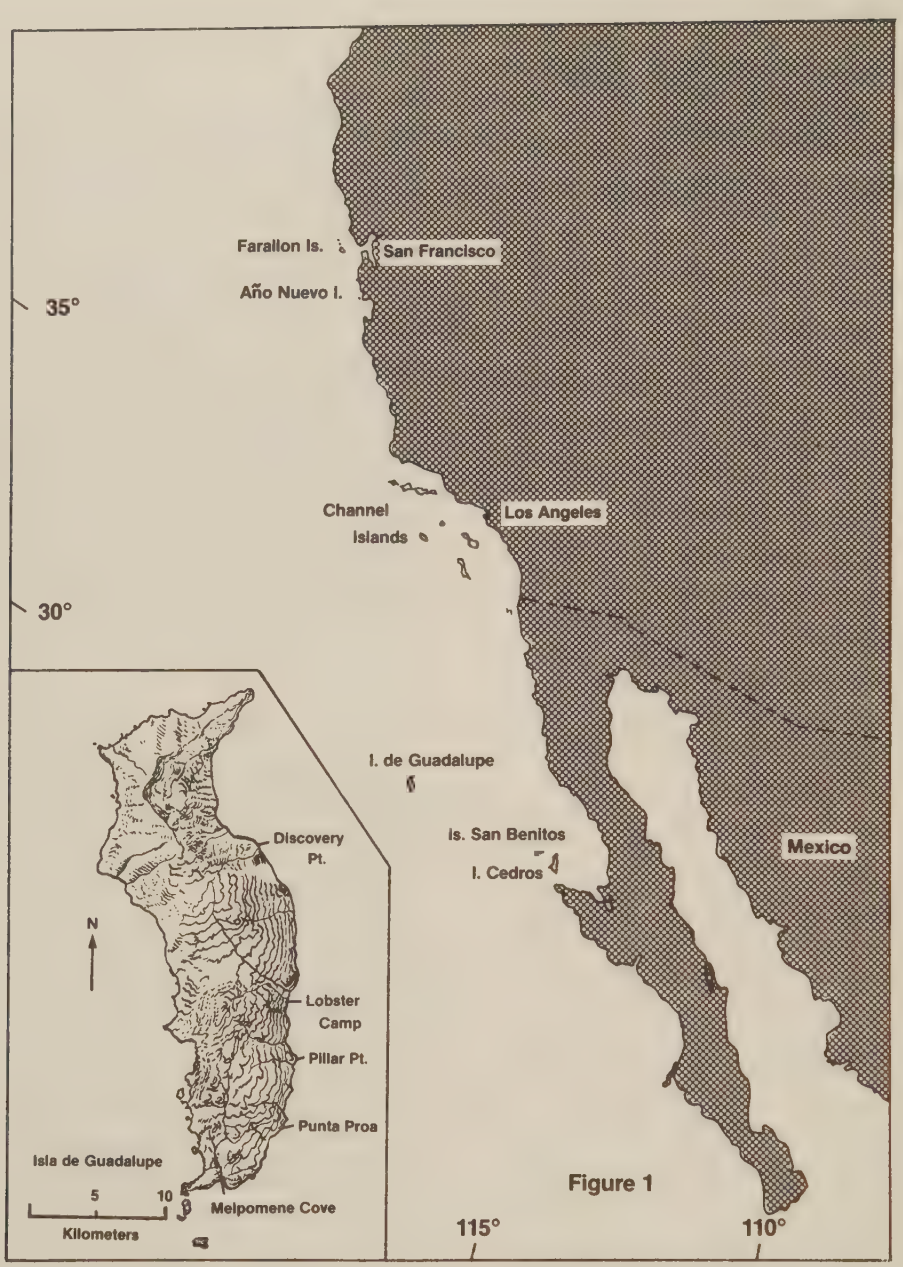


Figure 1—Isla de Guadalupe.

The eighth male contended for an already occupied territory on 12 June. He made three observed attempts to land on the territory between that date and 17 June, when he managed to establish himself elsewhere on the study area. All the interactions were vigorous postural and vocal displays without physical contact, and all ended with the intruder fleeing back into the sea. On June 17, he established himself in a small cove about 50 m south of the disputed territory. Although already occupied by another male, the cove was bisected by a large rock, and the two males were seldom in visual contact.

Territorial tenure and status of males—Between 17 June and 12 July, there were no changes in the study-area territories. All males were still on their territories, and none had been displaced, even temporarily. Thus, seven males held territory for at least 31 days, and one for at least 26 days.

On Isla de Guadalupe in both 1975 and 1977, fur seal males considerably smaller than their neighbors, and judged to be subadults, were observed holding territory in the middle of the breeding season. Although these territories were located near the periphery of the rookery, females were present on at least two of them.

The shoreline in most rookery areas was composed of broken volcanic rubble bounded by high cliffs, and the distance between cliff face and water was often less than 10 m. Territories were generally located on rocky surfaces; cobbled areas were normally occupied by breeding animals only in caves (exposed cobble or sand beaches were left to juvenile nonbreeders).

In the main study area, three of the coves were occupied by single males; the fourth cove was shared by two; and the territories of three males were situated on the point (Fig. 2). The eight territories varied in area from about 10 to 120 m^2; the mean was approximately 20 m^2. However, topography played a major role in determining territory size on this rookery; males were observed maintaining territories (on which females were also present) in crevices only a few square meters in area.

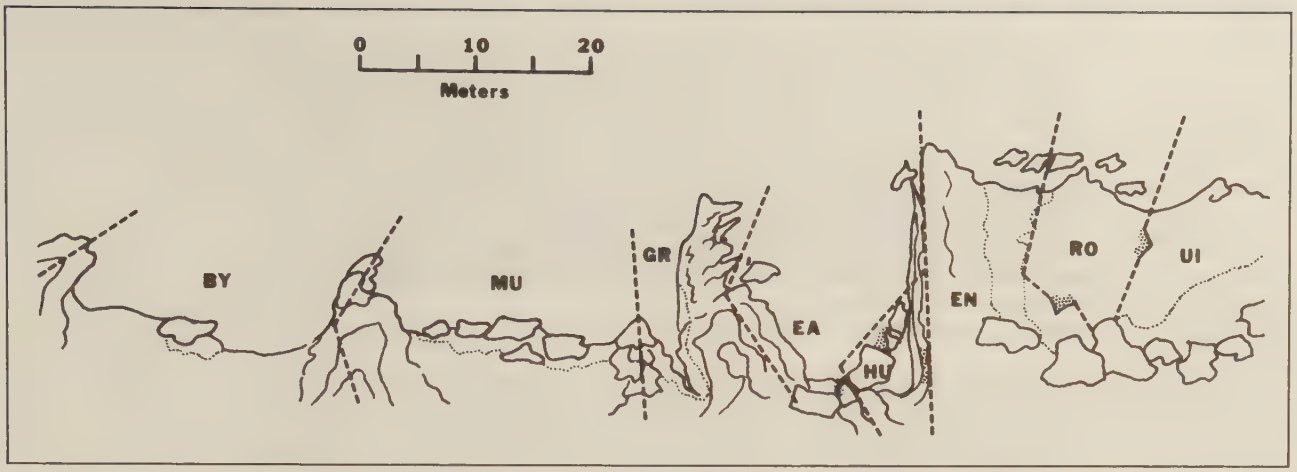


Figure 2—The 1975 main study area, showing approximate boundaries of the territories of eight *A. townsendi* males. Tidepools and high tide lines are depicted by dotted lines. Display sites are indicated by hash marks.

All territories observed here and elsewhere on the rookery fronted on the water. Most of the males were observed to enter the sea or tidepools connected to the sea daily, and no males were observed holding landlocked territories in the few areas where such space was available. Although no entirely aquatic territories were observed, some males obviously controlled the water immediately adjacent to their territories. On several occasions, bulls responded to the approach of other males to within 2-3 m of shore by diving into the water and attacking them. The intruding males always fled immediately without offering any resistance to the territory-holder.

Males occupying entire coves by themselves were generally out of sight of their nearest neighbors, from whom they were often separated by meters of rock. During a survey of the rookery in June 1968, Peterson and Ramsey (1970) estimated that no more than half of the territorial bulls were visible to their neighbors.

The territories in the study area remained unchanged in size and shape throughout the study. In great part, this was due to the fact that most territorial boundaries were defined by obvious physical features, such as rock walls or boulders. However, even territorial boundaries that extended across featureless rock remained constant; males encountering one another at a vague boundary of this sort always moved to certain topographically-defined display sites before beginning their threat displays (Fig. 2).

At least two of the eight males present on the main study area in 1975 were observed again in July 1977. These two males, identified by their vocalizations, were in the same locations that they had occupied two seasons previously. In June 1968, Peterson and Ramsey (1970) discovered an adult male fur seal on territory in a large cave located approximately 1 km north of Lobster Camp (Fig. 1). This male, named Lefty, was missing his left hindflipper. When the cave was relocated in June 1975, Lefty was present; he appeared healthy and maintained his territory throughout the study. He was again present in the cave in the summer of 1976, eight years after the initial sighting, but was missing in June 1977 (Fleischer 1978).

Presence of females—Two factors appeared to determine whether or not females would be present on a given territory. The first was cover: females were only observed on territories that had some sort of available cover, if only an overhanging ledge, under which they (and later their pups) could shelter from the sun. In 1975, the mean high (shaded) air temperatures recorded on the main study area reached a daily peak of 21.1°C at 1200 h. Some territories were completely enclosed in caves or crevices.

The second factor was access to water: territories with females had either a tidepool or a sheltered bit of shoreline. Females spent part of each day immersed and appeared to seek the water more actively than males. Tidepools were important during the early days of a female's stay on a territory, when her movements were most hindered by the resident bull. The two territories on the study area that remained empty of females throughout the study lacked both cover and unhindered access to water.

Due to the broken terrain and the fact that none of the animals were marked, the movements of most of the females in the study area could not be followed. Thus, it was difficult to determine exactly how many females were present on a given territory and to calculate an accurate sex ratio. Judging from observations of both females and pups, the male-to-female ratio was roughly 1:3. The greatest number of females observed on a territory at one time was 13; this territory was situated on a raised, naturally isolated rock platform, which contained a large central tidepool and ample cover.

On the Guadalupe rookery, roomy, open caves appear to provide the best combination of features attractive to females, and there is some evidence that these areas are first occupied by males: the adult male *Arctocephalus* observed on the island by R. S. Peterson (deceased, Univ. Calif. Santa Cruz) in early May 1967 were scattered widely along the shoreline and were, he felt, definitely attracted to sheltered cave entrance.

Fighting and boundary displays—No fights, defined here (after McCann 1980) as agonistic interactions in which the opponents attempt to physically overpower one another, were recorded between territorial males during these observations, which began when most adult males were already established on territories. Territorial males maintained the boundaries between themselves and neighboring bulls by means of mutual boundary displays consisting of series of sterotyped behaviors.

As reported by Peterson and Ramsey (1970), boundary displays always occurred at particular topographically well-defined locations: two males encountering one another at some other point along a territorial boundary would rush side-by-side to their display site before turning to face one another (Fig. 2). In some cases it was impossible to determine the exact boundary between two males, since most of it was never defended by display. Display sites were

often the only points of visual contact between males on semi-isolated territories, and some completely isolated males were never observed to interact with their neighbors. The eight territorial males on the main study area displayed at mean frequency of 0.23 displays per male per hour.

Figure 3 depicts a typical *A. townsendi* boundary display sequence. Upon reaching a display site, two males turned to face one another. One or both of the bulls lowered his chest (generally without contacting the ground) and lunged toward his opponent with open mouth. If one of the males was positioned above the other, he generally lowered his forequarters to compensate for the height difference. These lunges seldom resulted in physical contact; most thrusts ended with the heads of the males positioned about a third of a meter apart.

From this extended position, the two opponents rapidly waved their heads from side to side in an open-mouthed feinting motion. During this movement, as in the lunge, contact was carefully avoided. The head wave, which was performed at the rate of about 1 per second, occurred from 1 to 12 times in a single display sequence; a mean of 2.4 head waves was recorded in 214 displays.

The sequence was usually terminated, at least temporarily, when one or both of the males pulled his forequarters back, lifting and turning his head to stare obliquely away from his opponent. These oblique stares, first described for *Callorhinus* by Peterson (1965), were often followed by new sequences of lunges and head waves; they occurred in 16% of the observed interactions.

Boundary displays almost always ended when one or both of the bulls rotated his entire body to face completely away from his opponent. After several seconds in this position, the males would generally move away from the display site.

Physical contact was observed in only 5, or 2.1%, of 243 male-male interactions recorded during the 1975 study. In three instances, bites were inflicted during the course of mutual boundary displays; in each case, one of a displaying pair of males suddenly lunged and bit his opponent on the back or chest, causing him to retreat and ending the interaction. These incidents all involved the same two males.

The other two interactions involving physical contact followed the crossing of a territorial boundary. In both instances, the offending male entered a neighboring territory unobserved. Once discovered, the intruder's presence triggered an immediate attack from the resident bull. The intruder offered no resistance while on his neighbor's territory and, in both cases, was bitten on the hindquarters while fleeing back to his own ground.

Boundary displays varied in duration from short, succinct exchanges of less than 10 seconds to extended sequences lasting many minutes. Most of the latter were actually composed of several display sequences linked by periods of inactivity (usually 1-3 minutes), during which males maintained their display positions. In these situations, it was very difficult to determine where one display ended and another began. For example, in one 18-minute interaction, 11 minutes passed with the two males sitting opposite one another at the display site (generally in the oblique stare position).

Postures and vocalizations from neighboring males were obviously important in initiating boundary displays. On the main study area, five males that were in constant or frequent visual contact with their neighbors were observed to interact an average 0.36 times per hour, while three isolated males displayed a mean of only 0.01 displays per hour (t_6=4.17, P<0.01).

The two males whose territories lacked females throughout the 1975 study interacted with their neighbors an average 0.46 times per hour; the six males whose territories sheltered females displayed at the lower rate of 0.16 times per hour, a difference that was not quite significant at the 0.05 level (t_6=2.09).

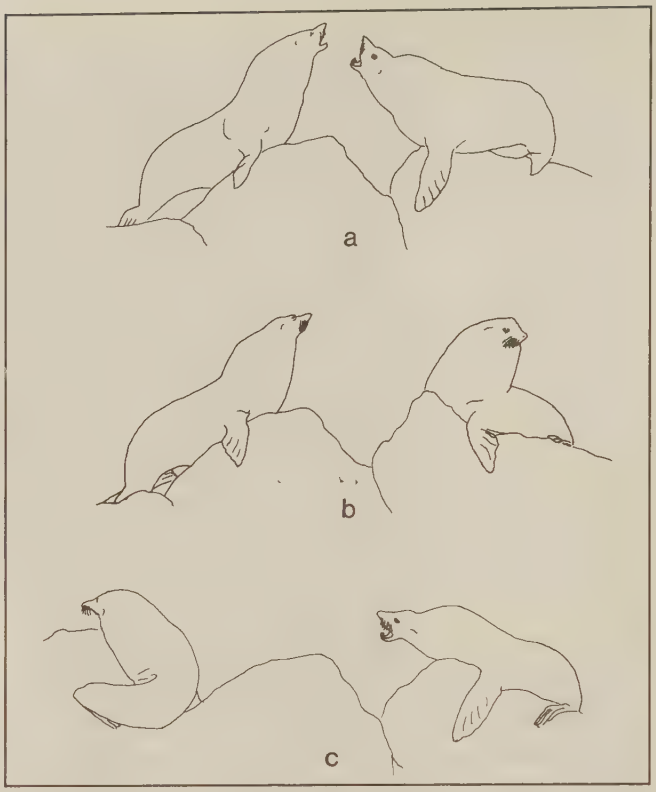


Figure 3—*A. townsendi* boundary display sequence. (a) Lunge; (b) oblique stare; (c) face away (left), lunge (right).

Vocalizations—Male Guadalupe fur seals are very vocal during the breeding season, and their vocalizations are integral parts of all male-male interactions. At least four distinct vocalizations are given in these and other contexts by males; these vocalizations are described below. Unless otherwise noted, the terms are those applied by Stirling and Warneke (1971) in their paper describing and comparing *Arctocephalus* vocalizations.

Full threat call—This is a long, drawn-out vocalization, which averages approximately 2 seconds in duration. There is apparently great variation in this vocalization in *A. townsendi*: the full threat calls of the males on the main study area differed considerably in quality, and individual bulls were easily recognizable by their threat calls. Figure 4 presents sonagrams of the full threat calls of four territorial males. To the human ear, the calls ranged in quality from an almost pure, musical tone (male RO) to a hoarse mule-like bray (male UI). Most of the threat calls fell between these two extremes in tonal quality.

This vocalization was characterized as high-intensity threat by Stirling and Warneke (1971). It certainly indicates a male's presence on territory and his readiness to display (or fight), and is commonly accompanied by a distinct head-up posture. The full threat call was generally employed over fairly long distances. It was given spontaneously, in response to vocalizations from other males (generally to other full threat calls), and during male-male interactions. It was often given directly preceding or following a mutual threat display; full threat calls occurred in 14% of the observed boundary displays.

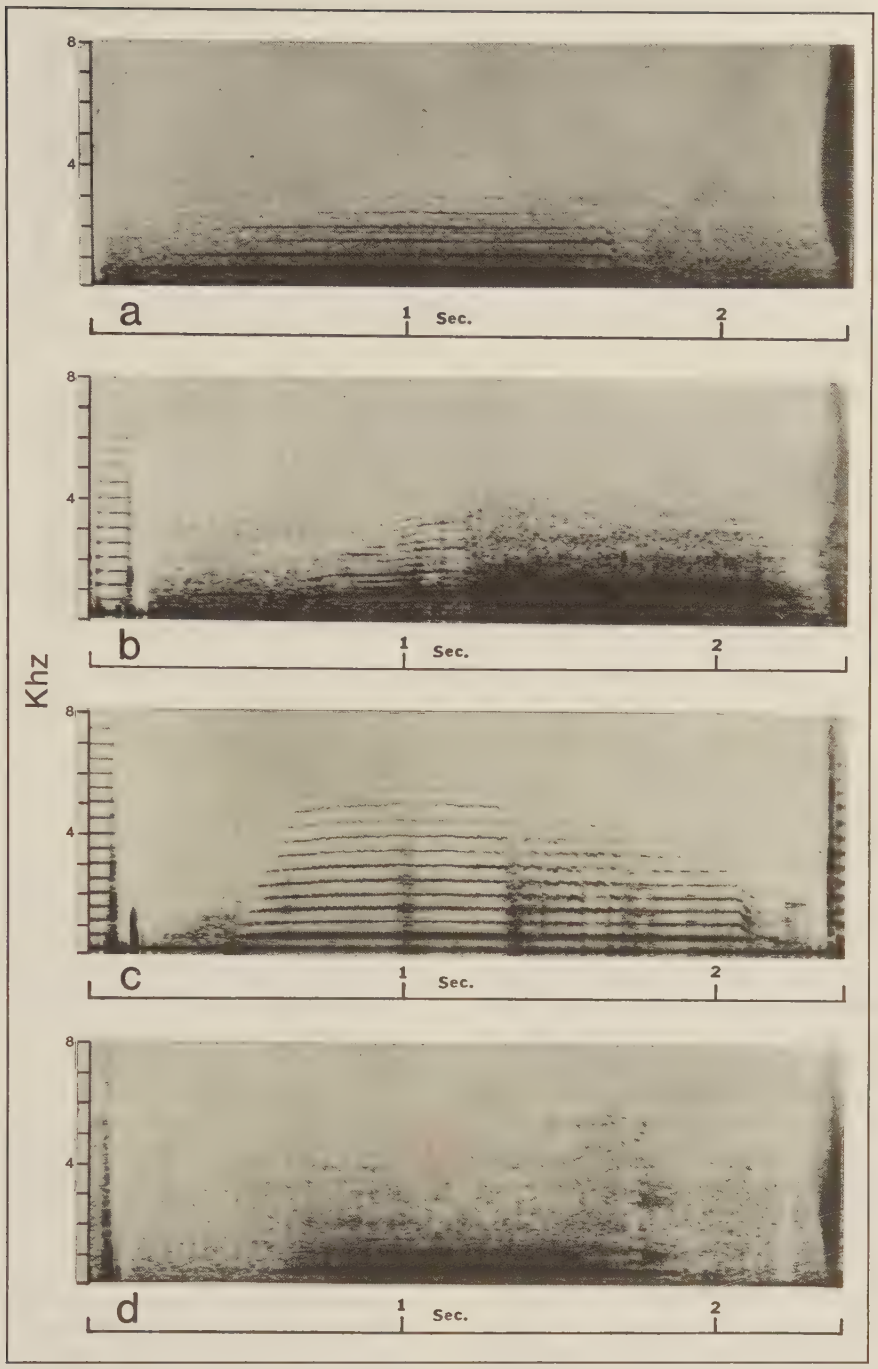


Figure 4—*A. townsendi* male full threat call. (a) Male RO; (b) Male UI; (c) Male MU; (d) Male EA.

***Boundary puff* (*Bartholomew 1953*)**—This is the vocalization termed the "male gutteral challenge" by Stirling and Warneke (1971). There is apparently some variation in this vocalization among the *Arctocephalus* species. In *A. townsendi*, as in *A. pusillus doriferus* and *Callorhinus*, it consists of a single sharp exhalation of air, which results in a harsh, puffing sound (Fig. 5a).

The boundary puff signifies a high-intensity threat. It was always given in conjunction with a belly-down lunge toward an opposing male during mutual threat displays.

Barking—The male bark was first clearly described for this species by Peterson et al. (1968). It is a low, repetitive call, with a somewhat nasal and whickery quality. It can vary greatly in rate, duration, and volume, depending on the behavioral setting. Like the samples of male barking recorded for *A. forsteria* and *A. gazella* (Stirling and Warneke 1971), it has quite clearly defined harmonics, but is lower in frequency. It also displays the high-frequency "shadow" first reported by Peterson et al. (1968; Fig. 5b).

The intensity of threat implied by this vocalization appeared to vary with context. It was the basic "patroling" vocalization, accompanying nearly every movement of a male about his territory. It was also given with increased intensity during male-female interactions or in response to vocalizations from other males, and at an almost frantic rate during boundary displays.

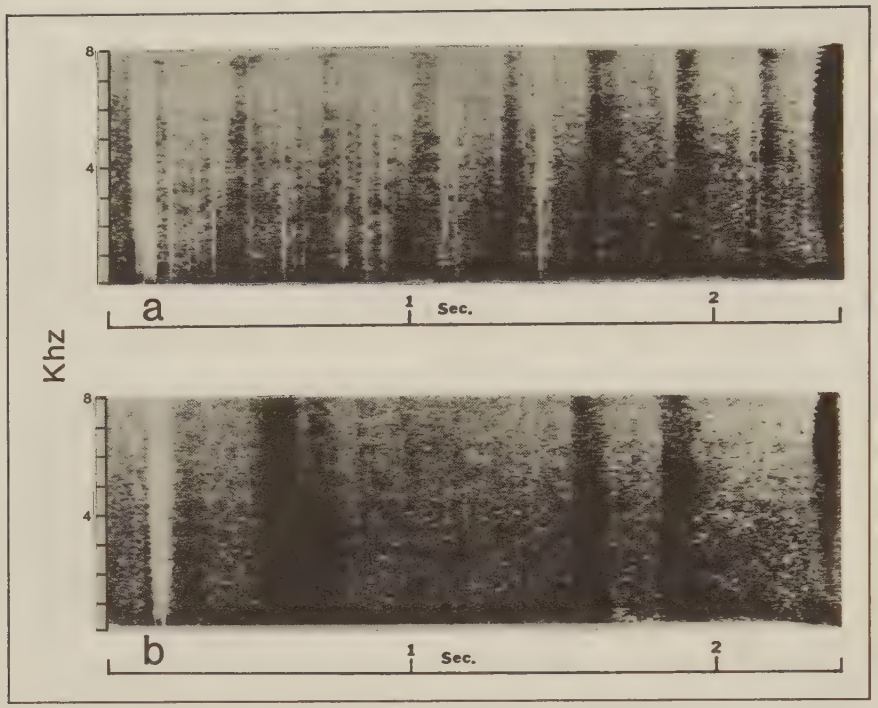


Figure 5—*A. townsendi* (a) male whicker-bark; (b) male boundary puff.

***Growl vocalization* (*this study*)**—This vocalization, termed a .ough by Peterson et al. (1968), consists of a low, gutteral sound, which may vary in duration and volume. It appears to be similar to the vocalization described for *A. forsteri*, *A. gazella*, and *A. tropicalis* and termed the "male low-intensity threat" by Stirling and Warneke (1971). It may simply be the first portion of the full-threat call. The growl vocalization was not tape-recorded during this study.

In *A. townsendi*, this vocalization varies from a low- to a high-intensity threat; males gave this call when interacting with females, in response to distant vocalizations from other males, during boundary displays and at the approach of humans. It was generally employed at close range.

The male (and female) submissive call, described by Stirling and Warneke (1971) as being common to all *Arctocephalus* species, was not heard during this study.

Male-female interactions—Female fur seals were already present on the main study area on 12 June, and more continued to arrive over the next two weeks. The high count of 10 females was first made on 17 June. However, considering the difficulty of locating and following unmarked animals on the rugged Guadalupe shoreline, it is possible that twice as many females were present on the main study area during the course of the study.

Almost 94% of the observed interactions between males and females were agonistic in nature. These generally involved attempts by territorial males to herd or make olfactory investigations of females, or both, and were almost invariably initiated by males. About 2% of the observed interactions, initiated by females, were outwardly ambiguous, and may have been preliminary approaches to males by pre-estrous females. Overtly sexual interactions, including precopulatory and copulatory behavior, accounted for the remaining 4% of the observed interactions; about three-quarters of these were also initiated by females.

Males were extremely aware of and attentive to females on their territories. Even when resting, they positioned themselves seaward of females and reacted to nearly every female movement across their territories. These male responses varied in intensity from a few whicker-barks emitted from a prone position to rapid intercepting movements, which usually ended in an attempt to block the female's path and make an olfactory investigation of her facial and perineal regions.

Males appeared to follow newly arrived females more closely. In these situations, males seldom moved more than a few meters from the females, and they were aroused by very slight movements. Males entering the water during these initial periods of female presence on their territories generally stayed in tidepools or within a few meters of shore.

Once aroused, a male moved to intercept the female that had attracted his attention, generally staying to seaward of her. A male whicker-barked while moving and, nearing a female, began moving his head from side to side (in what appeared to be a less intense version of the head-wave performed during boundary displays). Upon approaching a female, a male usually tried to touch noses with her briefly, then attempted an olfactory investigation of her perineal region.

Nonestrous females invariably reacted to the male aggressively, threatening with an open mouth (often giving a low growl) and swinging their hindquarters directly away. Females were generally able to move a few meters away from the male after a single encounter of this kind. However, females that held their ground and vigorously resisted the male's attentions often triggered a more intense response from the male, who would push the female with his forequarters, whicker-barking and head-waving with increasing frequency, and physically harass her until she backed down. Occasionally, a male remained at the spot vacated by the female, sniffing at the rocks on which she had been resting.

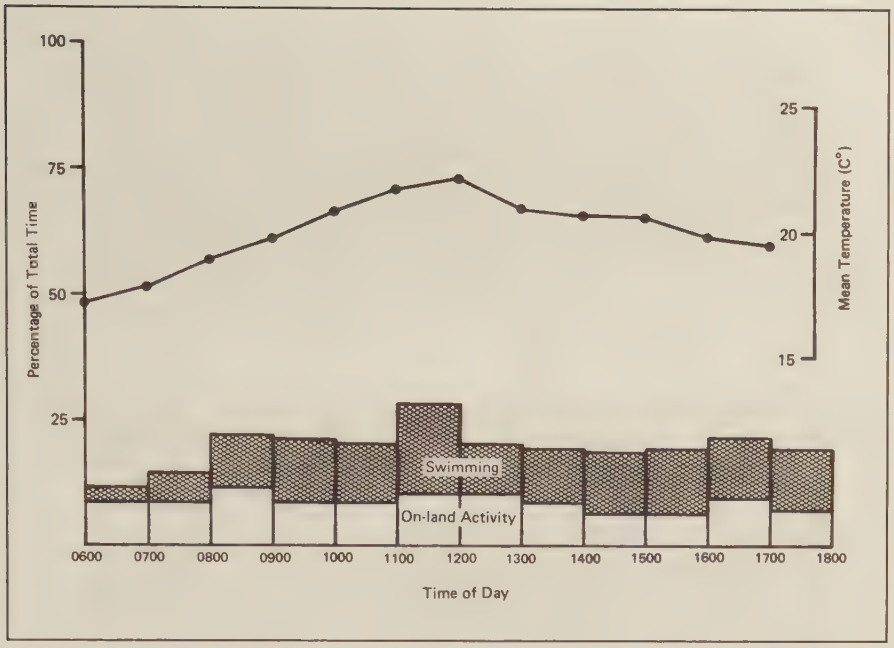


Figure 6—Daily pattern of male *A. townsendi* activity and mean hourly air temperatures.

Most of the interactions between territorial males and females involved herding as well as investigatory behavior. Males attempted to prevent females from leaving their territories or going to sea by physically blocking their movements and trying to direct them back towards the middle of their territories. Females were often confronted in this manner when they were merely shifting their position a few meters or seeking a tidepool in the middle of the day. In the presence of human intruders, territorial males were observed to retreat to the edge of the sea and turn to face inland, positioning themselves to stop females from rushing into the water.

On two occasions, males dove into the sea after females that had appeared a few meters off their territories (pursued there by other males) and forced the females to haul out on their territories. In both instances, the males exhibited vigorous herding behavior; they corralled the females and physically ushered them from the water.

Although territorial males appeared capable of controlling female movements, due in part to the low female densities and rookery topography, they could not prevent females from leaving their territories. Females went to sea quickly and quietly, slipping through the rocks and into the water without being seen by the territorial male.

Four copulations were observed in the main study area during the 1975 study. The first, observed on 20 June, involved a female that apparently had no pup and was noticeably smaller than the other two females present. This animal may have been nulliparous. The other copulations occurred on 29 and 30 June and 1 July, and involved females with pups. Only one copulation attempt was observed during the 1977 survey. This attempt, on 6 July, was the latest recorded and was apparently unsuccessful.

In all three cases in which precopulatory behavior was observed, the female was observed to initiate the interaction. The female approached the male and repeatedly nipped lightly at his neck and sides, often bringing her body into physical contact with his. Within 3 to 20 minutes in the observed cases, the male responded to these attentions by attempting to mount the female.

Females also appeared to terminate copulations. All observed copulations terminated within 30 seconds after the female began biting the male on his neck and abdomen. This behavior was actively aggressive toward the male, in contrast to female precopulatory behavior. The mean duration of the copulations observed was 15 minutes and 55 seconds (with a range of 10 min. 30 sec. to 28 min. 30 sec.).

Male-juvenile interactions—On Isla de Guadalupe, immature fur seals, including subadults and immatures of both sexes, were usually restricted to areas not occupied by breeding animals, and no female-yearling pairs were seen. One such area was Lobster Camp cove (Fig. 1), located immediately south of the main study area. This area was occupied by 60 to 80 fur seals that appeared to be immature animals of several year classes (Fleischer 1978). No obvious bachelor lairs of subadult males were observed. These nonbreeders comprised the most active segment of the population, spending a good part of each day swimming or interacting in the surf.

Immature fur seals, particularly subadult males, occasionally appeared in the main study area. They often floated a few meters offshore with heads raised well out of the water, surveying the nearby rocks. If a territorial bull was visible on the shore, the intruding juvenile or subadult invariably swam away.

Territorial males always threatened juveniles or subadults that they discovered hauled-out on their territories, but their reactions varied in intensity. The most common response to an intrusion of this sort was a rather low-level threat; whicker-barking, the bull slowly approached until the trespasser dashed into the sea. On a few occasions, adult males rushed after fleeing juvenile fur seals, attempting to bite them on the hindquarters, and even pursuing them into the water. Intruders eliciting this reaction from territorial males were subadults large enough to possess obvious male characteristics.

Daily patterns—The level of male activity on land (including all movements, vocalizations, and interactions with other individuals) remained fairly constant between 0600 and 1800 h, accounting for 6 to 10% of total observation time and showing no definite daily cycle (Fig. 6). Swimming accounted for 3-18% of the observed activity, peaking about midday and remaining at a relatively high

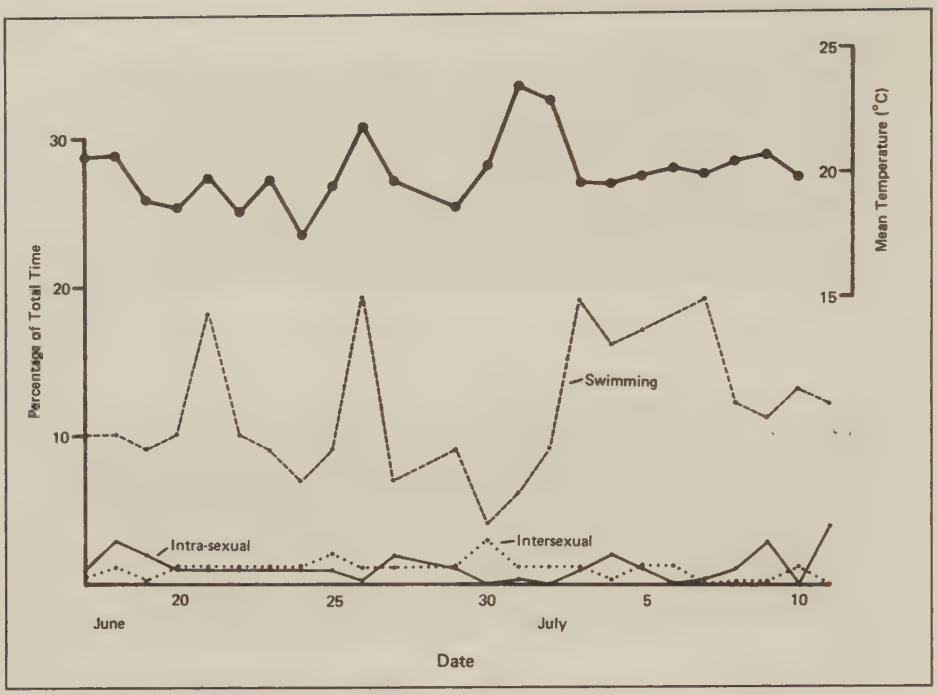


Figure 7—Seasonal pattern of male *A. townsendi* activities and mean daily air temperatures.

level throughout the afternoon. There was a strong positive correlation between time spent in the water and the hourly mean air temperatures recorded on the main study area ($t_{10}=4.35$, $P<.01$).

Upon entering the water, males commonly swam 5-15 m from shore and began grooming. Males whose territories contained females seldom ventured farther than 10 m from shore, especially during the first few days after the females had arrived. One male, whose territory centered around a large, protected tidepool, was observed to go to sea only once, late in the study, when females were no longer present on his territory. Males whose territories lacked females swam farther out and along the shore, and often disappeared for periods of a few minutes to several hours.

Frequency of boundary displaying showed a weak negative correlation with mean air temperature throughout the day ($t_{10}=1.59$, $P>.1$). Display frequency rose to a peak in midmorning (0900-1000 h), then declined to a low in midafternoon (1400-1500 h). Mean air temperatures recorded from a shaded thermometer mounted above the study area were highest at 1200 h (mean temperature recorded at 1200 h was 21.1°C). However, ambient temperatures were probably highest down on the shoreline rocks in midafternoon, when reradiation of heat from the substrate was greatest.

Seasonal patterns—The general low level of male activity was maintained throughout the study (Fig. 7). Males in both the main and cave study areas were active during 20% of the hours of observation; of this active time, 11% was spent swimming, 7% in movement on territory, and 2% in direct interactions with other individuals (both males and females). No significant correlation was found between these activities and mean daily air temperature.

For the period 29 June through 11 July, the activity pattern of a male located on an exposed territory in the main study area was compared with that of a male whose territory was enclosed in the cave study. The main-area male was active 26% of the observation time during this period; swimming accounted for 20%, movement on territory for slightly less than 5%, and interactions with other individuals for approximately 1%. The cave-area male was active 21% of the observation time; he spent 9% of the time swimming, approximately 10% in movement about his territory, and somewhat less than 2% in interactions with other individuals. Thus, the male with the exposed territory spent more time in the water, but was less active on land than the male whose territory was sheltered in a cave.

Female behavior

Although a few females were already present on the Guadalupe rookery when observations began on 12 June 1975, the major influx of females began in the third week of June, and females continued to arrive throughout the month. Many females appeared to land at night or very early in the morning; most new arrivals in the main study area were sighted between 0600 and 0630 h. However, females did haul out on the rookery throughout the day.

Adult females were gregarious. As Peterson and Ramsey (1970) reported, females arriving on a territory generally moved toward any females already present, and females tended to aggregate. There were limits to this gregariousness, however; the approach of a female to within about 1 m of another almost invariably resulted in an aggressive interaction between the two. Females always threatened one another with opened mouths, often emitting low, growling threat vocalizations. These encounters usually lasted only a few seconds, ending when one of the females backed off and moved away. No physical contact was observed during these interactions.

Territorial males often reacted to female-female interactions by rushing over and attempting to investigate both the participants. Females interrupted in this manner would immediately turn to confront the intruding male, threatening him with opened mouths and backing away.

Parturition—Before parturition, females were relatively inactive on land. They spent most of the daylight hours sleeping or groom-

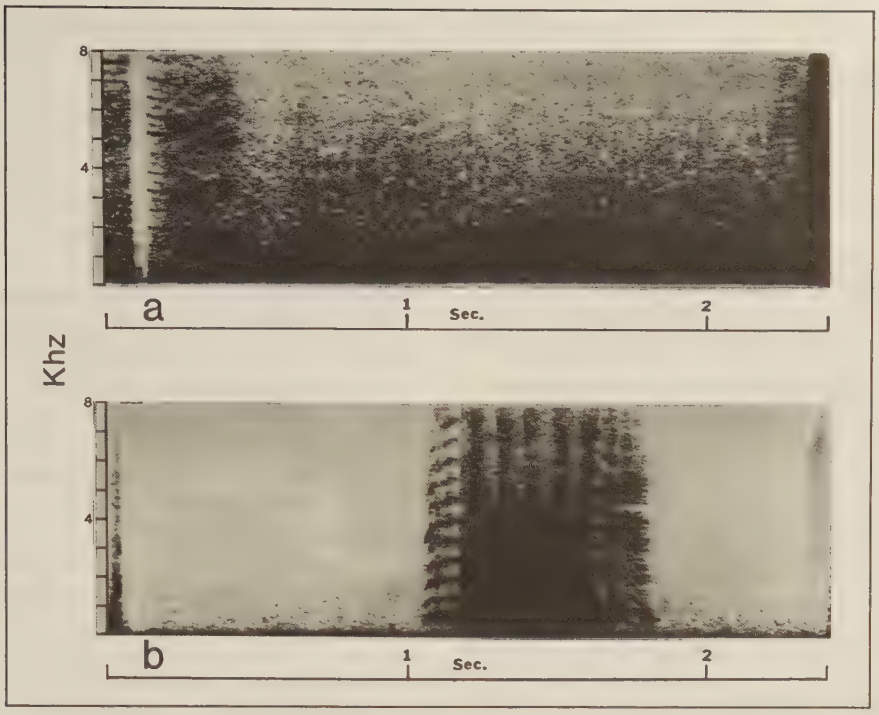


Figure 8—*A. townsendi* (a) pup attraction call and (b) female attraction call.

ing quietly, generally moving only to avoid males or to enter tidepools. Although no births were observed, the approximate period between arrival and parturition was determined for five females: the range was 2.5 to 6 days, with a mean of approximately 4 days. In June 1968, Peterson and Ramsey (1970) recorded a birth 30 hours (or 1.25 days) after the arrival of the female.

In 1975, the first pup detected was heard (but not seen) on 14 June. The first pup observed on the main study area was born on 16 June, and other pups were probably born in the main and cave study areas on 17, 19 (two births), 23, 26, 27, and 29 June. The two births observed by Peterson and Ramsey (1970) in 1968 occurred on 25 and 29 June. Pupping had apparently passed its peak by the end of June, but births occurred at least until the end of July; the latest birth reported by Fleischer (1978) occurred on 22 July 1976.

On 26 June 1975, a freshly expelled placenta was observed at 0900 h, indicating that the pup had been born between 0800 and 0900 h. The two births reported by Peterson and Ramsey (1970) occurred at approximately 1000 and 1250 h, respectively.

R. S. Peterson (deceased, Univ. Calif. Santa Cruz, unpubl. data) described a birth that occurred on 25 June 1968. When the female first attracted his attention, she was vocalizing, giving the low-pitched pup attraction call (first described for *A. townsendi* by Peterson et al. 1968; Fig. 8a). The female turned and nuzzled her perineum, then began circling slowly. That was apparently the onset of labor; the pup was born 3.5 minutes later in a cephalic presentation.

At birth, the pup's eyes were open and its movements were clumsy, but vigorous. It began vocalizing within 15 seconds after birth, emitting the bleating female attraction call (Stirling and Warneke 1971; Fig. 8b). After a brief delay, the female answered with pup attraction calls. She grasped the pup several times with her mouth without lifting it as it nuzzled at her belly. The placenta was expelled 32 minutes after the pup had been born. Forty-four minutes after its birth, the pup appeared to be suckling successfully.

Maternal Behavior—Females were observed to nurse their pups as many as six times per day, although they averaged about two bouts per day. The mean duration of observed nursing bouts was 18.5 minutes (none was observed to last longer than 33 minutes). Nursing bouts were generally intermittent rather than continuous.

When not nursing, females continued their usual activities of sleeping, grooming, and lolling in tidepools, and interacted very little with their pups. They often wandered 5-10 m away from their pups and could be very slow in responding to their vocalizations. At times, females simply remained where they were and answered their pups' cries with attraction calls, forcing the pups to crawl to them. Females did make efforts to move their pups out of the surf, often picking them up in their teeth and carrying them upslope.

Females behaved aggressively toward pups other than their own. After sniffing a pup and determining that it was not her own, a female would immediately threaten it. On several occasions, females were observed to bite alien pups. One pup was picked up bodily and thrown by a female that it had approached.

Figure 9 depicts the time spent on the rookery by six females during the 1975 breeding season. Each female's stay on the rookery is followed from her arrival to her first departure to sea to feed and, in three cases, to her first return to the rookery. The dates of parturition are indicated where known.

The observed period between parturition and copulation ranged from 5 to 10 days, with a mean of 7.3 days. One female left the day after she copulated; two others remained with their pups for at least two days before departing.

The length of time spent at sea on the first feeding trip was determined approximately for three females, ranging from 2 to at least 5 (and probably 6) days. A pup on Peterson's 1968 study area remained alone and unfed for at least 7 days (R. S. Peterson, deceased, Univ. Calif. Santa Cruz, unpubl. field notes).

Mutual recognition between mother and pup was apparently achieved by means of vocalizations and, at close range, by olfac-

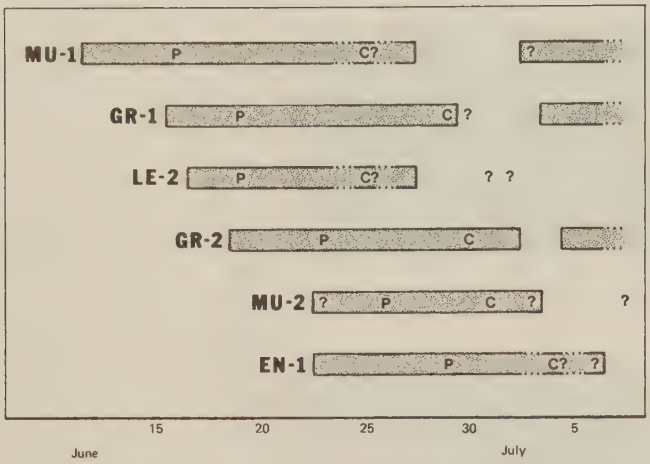


Figure 9—Time spent on the rookery by six female *A. townsendi*. P = parturition; C = copulation.

tory communication. Females approached by alien pups always investigated by sniffing before repulsing them.

The timing of subsequent feeding trips to sea and stays on land could not be determined during this study. This was mainly due to two reasons: the difficulty of following individual, unmarked females; and the presence of heavy storm-generated surf during much of the latter 2 weeks of the study. Storms caused many females to seek shelter in crevices or under rocks, and may have swept a few completely away. One female may have been back ashore for only 2 days before returning to sea on her second feeding trip.

This cycle of alternating feeding trips to sea and sojourns on land probably lasts for at least 8 months. Females and their pups appear to remain associated through the following winter, and a pup has been observed suckling as late as April (M. Bonnell and M. Pierson, Univ. Calif. Santa Cruz, unpubl. data).

DISCUSSION

Male territoriality

In general, the reproductive behavior of the Guadalupe fur seal appears to be quite similar to that reported for other species in the genus *Arctocephalus* (Vaz-Ferreira 1956; Paulian 1964; Rand 1967; Bonner 1968, 1981; Stirling 1970, 1971a,b; Stirling and Warneke 1971; Miller 1974, 1975; Gentry 1975; Warneke and Shaughnessy 1985).

Adult male Guadalupe fur seals presumably spend most of the year at sea, since they are absent from the island outside the breeding season. They begin arriving on Isla de Guadalupe in early May, and incipient territorial behavior has been observed at that time (R. S. Peterson, deceased, Univ. Calif. Santa Cruz, unpubl. data).

Fighting between *Arctocephalus* males occurs when they are contending for, expanding, or reclaiming territory (Gentry 1975; Miller 1975; McCann 1980; Bonner 1981; Warneke and Shaughnessy 1985). Since most of the *A. townsendi* adult males were already present on the rookery and established on territories when this study began on 12 June, it is not surprising that no fights were observed. If there had been a peak of fighting, it occurred at least a week earlier. Given the low breeding population density and the physical isolation of many territories, it is possible that many males acquire territories without fighting.

The observed level of boundary display activity engaged in by territorial *A. townsendi* males on the Guadalupe rookery is also relatively low. A mean rate of 0.23 displays per male per hour was recorded for the eight males on the main study area, while mean display rates of 0.6 displays per male per hour (*A. forsteri*; Gentry 1975) to 1.2 displays per male per hour (*A. gazella*; McCann 1980) have been reported for other *Arctocephalus* species.

It seems likely that apparently subadult males were able to maintain territories on the Guadalupe rookery because of the low population density. Continued increase in the size of the breeding population would probably result in the exclusion of younger males from rookery areas and in a general increase in the number and level of agonistic interactions between males.

Peterson (1965) recorded a mean of 47 days on territory for 16 adult male northern fur seals, *Callorhinus ursinus*, on the Pribilof Islands, while terms of tenure reported for *Arctocephalus* males of several species have been somewhat shorter, ranging from 34 to 38 days (Stirling 1971a; Gentry 1975; McCann 1980). The mean tenure of 29.5 days recorded in this study is obviously low; males probably abandon the rookery in late July or early August, and it is possible that the term of territorial tenure is in excess of 40 days.

However, the mean term of *A. townsendi* territorial tenure will probably shorten if the population continues to grow. The percentage of time spent in the water each day by territorial males, the strong correlation between time spent in the water and hourly recorded mean temperatures, and the observed differences in terrestrial activity levels between males on sheltered and unsheltered territories are all evidence that a certain level of thermal stress is associated with maintaining a territory on the Guadalupe rookery, even at present population levels. This, given a density-related increase in the intensity of male-male competition, should lead to a greater turnover of territorial males during the course of a breeding season.

In the *Callorhinus* breeding population on Robben Island studied by Bychkov and Dorofeev (1962), males held territory for significantly shorter periods of time than males in the St. Paul Island population studied by Peterson (1965). Peterson believed that much of this difference could be explained by the higher summer air temperatures on the Soviet rookery, which resulted in greater thermal stress on territory holders. A density-related increase in the intensity of male-male competition for territories under a more or less constant air temperature regime on the Guadalupe rookery should have the same effect. It should also make it unlikely that inland territories could be established on more than a temporary basis.

One male Guadalupe fur seal, Lefty, was possibly present at the same location for at least 9 consecutive breeding seasons—a long time for an otariid male to hold territory. Adult male *Callorhinus* on the Pribilof Islands generally hold territory for 3-4 years (Baker et al. 1970). On the Año Nuevo Island Steller sea lion (*Eumetopias jubatus*) rookery, the mean tenure is somewhat less, 2-3 years, although one male held the same territory for seven consecutive seasons (R. Gisiner, Univ. Calif. Santa Cruz, pers. commun.). Similarly, Warneke and Shaughnessy (1985) reported that *A. pusillus doriferus* may hold territory for as many as six consecutive seasons, but that the average male reproductive career lasts only 1.8 years.

Males of most *Arctocephalus* species reach sexual maturity at 4-5 years of age, but do not attain social maturity, or territorial

status, until 8-13 years, (Mattlin 1978; Payne 1979; Bonner 1981; Warneke and Shaughnessy 1985). The male Lefty was identified as an adult by Peterson and Ramsey (1970) when he was discovered in 1968; by 1976, the last year in which he was observed, he was probably at least 13 years old.

Breeding habitat

In contrast to the present distribution of *A. townsendi*, most otariids breed on the windward sides of islands, a tendency which presumably lessens the thermoregulatory stress associated with terrestrial activity (Paulian 1964; Peterson and Bartholomew 1967; Peterson and Ramsey 1970). Peterson and Ramsey (1970) suggested that the occupation of the east side of Isla de Guadalupe, which is sheltered from the rough seas found on the west side of the island, may reduce pup mortality. They also pointed out that most of the rookery areas on the eastern shoreline receive only morning sunshine, since the high cliffs block out much of the hotter afternoon radiation. Another possible explanation for the present distribution of *A. townsendi* is simply that the surviving remnant of the population inhabited the east side of the island and, because of its strong site tenacity, the population has not yet spread to the west side.

The breeding population is scattered along the length of the rookery and, in most areas, the density is quite low. This is partially due to the small population size. However, as discussed by Peterson and Ramsey (1970) other otariid populations have tended to haul out in dense aggregations even when few in number (Osgood et al. 1915; Csordas and Ingham 1965).

Peterson et al. (1968) suggested that there may have been some selection for shy and secretive individuals during the period of intensive sealing during the nineteenth century, and that these seals survived to form the nucleus of the present breeding population. Although some selection for individuals exhibiting these behavioral traits may have occurred, the results of this study indicate that the present, scattered distribution is due primarily to the small population size and the topography of the stretch of shoreline now occupied.

It has been suggested that the presence of extensive areas of highly polished shoreline rock on Isla de Guadalupe indicates that the fur seals once occupied shoreline on both sides of the island in great numbers and, presumably, in dense aggregations (Bartholomew and Hubbs 1952; Hubbs 1956; Peterson et al. 1968). The species' well-defined sexual dimorphism (adult males weigh roughly three times as much as adult females; Fleisher 1978) is also evidence that vigorous male-male competition for territories and access to females and a fairly high degree of polygyny existed in the past (Peterson and Bartholomew 1967; Peterson 1968; Bartholomew 1970).

If the population continues to grow, I would expect the species' social organization to change in that direction. As density on the rookery increases, within the limits afforded by the topography of the Guadalupe shoreline, the intensity of male-male competition will also increase, resulting in greater turnover of territorial males and shorter average tenure. Subadult males will no longer successfully hold territory in the rookery.

Fur seals will probably begin breeding in suitable areas on the windward west side of the island, and will continue to appear on the California Channel Islands with increasing frequency. Eventually, they may reestablish a breeding colony on the Channel Islands, where they once occurred in considerable numbers (Walker and Craig 1979).

CITATIONS

BAKER, R. C., F. WILKE, and C. H. BALTZO.
1970. The northern fur seal. Circ. 336, U.S. Dep. Int., Fish Wildl. Serv., Wash., D.C., 19 p.

BARTHOLOMEW, G. A., Jr.
1953. Behavioral factors affecting social structure in the Alaska fur seal. *In* Trans. 18th N. Am. Wildl. Conf., p. 481-502.
1970. A model for the evolution of pinniped polygyny. Evolution 24:546-559.

BARTHOLOMEW, G. A., Jr., and C. L. HUBBS.
1952. Winter population of pinnipeds about Guadalupe, San Benito, and Cedros islands, Baja California. J. Mammal. 33:160-171.

BONNER, W. N.
1968. The fur seal of South Georgia. Br. Antarct. Surv. Sci. Rep. 56, 81 p.
1981. Southern fur seals *Arctocephalus* (Geoffrey Saint-Hilaire and Cuvier, 1826). *In* Ridgay, S. H., and R. J. Harrison (eds.), Handbook of marine mammals, Vol. 1, p. 143-160. Academic Press, London.

BYCHKOV, V. A., and S. V. DOROFEEV.
1962. On the behavior of fur seal bulls during the harem period. Zool. Zh. XLI (9):1433-1435.

CSORDAS, S. E., and S. E. INGHAM.
1965. The New Zealand fur seal, *Arctocephalus forsteri* (Lesson), at Macquarie Island, 1949-64. CSIRO Wildl. Res. 10:83-99.

FLEISCHER, L. A.
1978. The distribution, abundance, and population characteristics of the Guadalupe fur seal, *Arctocephalus townsendi* (Merriam, 1897). M.S. Thesis, Univ. Wash., 93 p.
1987. Guadalupe fur seal, *Arctocephalus townsendi*. *In* Croxall, J. P., and R. L. Gentry (eds.), Status, biology, and ecology of fur seals, p. 43-48. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 51.

GENTRY, R. L.
1975. Comparative social behavior of eared seals. Rapp. P.-v. Reun. Cons. int. Explor. Mer 169:189-194.

HUBBS, C. L.
1956. Back from oblivion. Guadalupe fur seal: still a living species. Pac. Discovery 9:14-21.

MATTLIN, R. H.
1978. Pup mortality of the New Zealand fur seal (*Arctocephalus forsteri* Lesson). N.Z. J. Ecol. 1:138-144.

McCANN, T. S.
1980. Territoriality and breeding behavior of adult male Antarctic fur seals, *Arctocephalus gazella*. J. Zool. (Lond.) 192:295-310.

MILLER, E. H.
1974. Social behavior between adult male and female New Zealand fur seals, *Arctocephalus forsteri* (Lesson) during the breeding season. Aust. J. Zool. 22:155-173.
1975. Social and evolutionary implications of territoriality in adult male New Zealand fur seals, *Arctocephalus forsteri* (Lesson, 1828), during the breeding season. Rapp. P.-v. Reun. Cons. inst. Explor. Mer 169:170-187.

OSGOOD, W. H., E. A. PREBLE, and G. A. PARKER.
1915. The fur seals and other life on the Pribilof Islands, Alaska. Bull. U.S. Bur. Fish. 34, Doc. 820, 172 p.

PAULIAN, P.
1964. Contribution a l 'etude de l'otarie de l'Ile Amsterdam (A contribution to the study of the Amsterdam Island fur seal). Mammalia 28 (Suppl. 1):1-146.

PAYNE, M. R.
1979. Growth in the Antarctic fur seal *Arctocephalus gazella*. J. Zool. (Lond.) 187:1-20.

PETERSON, R. S.
1965. Behavior of the northern fur seal. Ph.D. Thesis, Johns Hopkins Univ., Baltimore, 214 p.
1968. Social behavior in pinnipeds, with particular reference to the northern fur seal. *In* Harrison, R. J., R. C. Hubbard, R. S. Peterson, C. E. Rice, and R. J. Shusterman (eds.), The behavior and physiology of pinnipeds, p. 5-53. Appleton-Century-Crofts, New York.

PETERSON, R. S., and G. A. BARTHOLOMEW.
1967. The natural history and behavior of the California sea lion. Am. Soc. Mamm. Spec. Publ. 1, 79 p.

PETERSON, R. S., and D. H. RAMSEY.
1970. Reproductive behavior of the Guadalupe fur seal. *In* Proc., Sixth Annu. Conf. on Biological Sonar and Diving Mammals, p. 23-28. Stanford Res. Inst., Menlo Park, Calif.

PETERSON, R. S., C. L. HUBBS, R. L. GENTRY, and R. L. DeLONG.
1968. The Guadalupe fur seal: habitat, behavior, population size, and field identification. J. Mammal. 49:665-675.

RAND, R. W.
1967. The Cape fur seal. 3. General behavior on land and at sea. S. Afr. Div. Sea Fish. Invest. Rep. 60:1-39.
STIRLING, I.
1970. Observations on the behavior of the New Zealand fur seal (*Arctocephalus forsteri*). J. Mammal. 51:766-778.
1971a. Studies on the behavior of the South Australian fur seal, *Arctocephalus forsteri* (Lesson). I. Annual cycle, postures and calls, and adult males during the breeding season. Aust. J. Zool. 19:243-266.
1971b. Studies on the behavior of the South Australian fur seal, *Arctocephalus forsteri* (Lesson). II. Adult females and pups. Aust. J. Zool. 19:267-273.
STIRLING, I., and R. M. WARNEKE.
1971. Implications of a comparison of the airborne vocalizations and some aspects of the behavior of the two Australian fur seals, *Arctocephalus* spp. on the evolution and present taxonomy of the genus. Aust. J. Zool. 19:227-241.
VAZ-FERREIRA, R.
1956. Etologia terrestre de *Arctocephalus australis* en las islas Uruguayas (Terrestrial ethology of *Arctocephalus australis* on Uruguayan islands). Ministerio de Industrias y Trabajo, Servicio Oceanographico y de Pesca — Trabajos sobre islas de lobos y lobos marinas, No. 2:3-22.
WALKER, P. L., and S. CRAIG.
1979. Archaeological evidence concerning the prehistoric occurrence of sea mammals at Point Bennett, San Miguel Island. Calif. Fish Game 65:50-54.
WARNEKE, R. M., and P. D. ShAUGHNESSY.
1985. *Arctocephalus pusillus*, the South African and Australian fur seal: taxonomy, evolution, biogeography, and life history. *In* Ling, J. K., and M. M. Bryden (eds.), Studies of sea mammals of south latitudes, p. 53-77. Proc. 52nd ANZAAS Congr., Sydney, May 1982. South Aust. Mus.

Behavioral Cues to Individual Recognition in the Subantarctic Fur Seal, *Arctocephalus tropicalis*

JEAN-PAUL ROUX[1]
Institut des Sciences de l'Evolution
Section Socioecologie
U.S.T.L. Place Bataillon
34060 Montpellier Cedex
France

PIERRE JOUVENTIN
CEBAS-CNRS
79369 Beauvoir-sur-Niort
France

ABSTRACT

During the breeding season, individual recognition was studied in different age groups and sex classes of the subantarctic fur seal *Arctocephalus tropicalis* on Amsterdam Island. Of all the possible cues, vocal signals are the most important. Detailed analyses of the behavioral sequences, together with playback experiments in the field, show that individual recognition occurs between the females and their pups and also between the territorial males. The biological significance of this is discussed.

INTRODUCTION

Fur seals generally breed in high-density colonies. The duration of the suckling period for pups is long, lasting from several months to more than 1 year according to the species. During this period the pups are land based, while the females alternate between feeding trips at sea and suckling attendance on shore.

Observations of most species of fur seals suggest the existence of an elaborate recognition system between mothers and their pups: *Callorhinus ursinus* (Bartholomew 1959), *Arctocephalus forsteri* (Stirling 1971b; Stirling and Warneke 1971; McNab and Crawley 1975), *A. tropicalis* (Paulian 1964; Bester 1977), *A. galapagoensis* (Trillmich 1981), *A. australis* (Trillmich and Majluf 1981), and *A. townsendi* (Pierson 1987). Most authors agree that mothers seem to take a more active part in the recognition process than the pups, but Trillmich (1981) gave evidence (playback experiments) that the pups of *A. galapagoensis* can recognize their mothers' vocalizations. Although the ability of the fur seal mothers to recognize their own pups is obvious in the field, neither experimental proof nor studies of the different cues and mechanisms involved have been published. The existence of individual recognition between adult males has been suggested in *A. forsteri* (Stirling 1971a). Our paper presents some preliminary results from a study of individual recognition processes in *A. tropicalis*.

STUDY SITE AND METHODS

Behavioral studies of *A. tropicalis* were carried out on Amsterdam Island (lat. 37°50′S, long. 77°35′E) from September 1981 to March 1982. The Amsterdam Island population is recovering from overexploitation during the last century. Within the 1981-82 breeding season, 35,000 fur seals hauled out on Amsterdam Island (Hes and Roux 1983). Almost the entire coastline of the island (28.5 km) is used by the seals, and breeding colonies occupied 81% of the coastline in 1982 (Roux 1987), where nearly 11,000 pups were born (Roux 1982).

The study colonies were situated along the north coast and have the typical island biotope (jumbled rocks and rocky platforms backed by cliffs). The density of seals on these colonies was medium to high for the island (Roux 1987).

Two metal tags bearing the same number were attached to the trailing edge of the pups' fore flippers. Some pups' backs were also marked with enamel paint spots (green or orange). Adult males and females, which could not be individually recognized by means of wounds or scars, were marked with enamel paint spots on the back or on the base of the fore flippers.

Prior to the arrival of the females, the territorial status of the males was determined by direct observation of male interactions and charging behavior.

A Uher 4000 Report portable tape recorder was used for the sound recordings at a tape speed of 19 cm/s with a Beyer Dynamic M69N microphone or a Sennheiser MKH 815T directional microphone. All recordings were made from a distance of 1 to 6 m from the animals.

In the laboratory, calls were analyzed with a Kay Elemetrics Sonagraph 6061B using the linear scale and the 80-8,000 Hz frequency range. Filter resolution was 45 Hz for frequency measurements and 300 Hz for duration and temporal pattern measurements. The sectioner was used with 45-Hz filter resolution to quantify the relative amplitude levels of the different harmonics.

[1]Present address: Sea-Fisheries, P.O. Box 394, 9000 Luderitz, S.W.A./Namibia.

Playback experiments were effected on adult males, adult females, and pups in the breeding colonies using the internal amplifier of the Uher tape recorder connected to an Audax loudspeaker with a 12-m coaxial lead.

Playback experiments on males were made in November 1981, after they had established their territories and before the colony became crowded with females and pups. During this period adult males represented about 60% of the animals on the breeding colonies, most of them being territorial (Roux and Hes 1984). Two colonies of similar structure and territory density, 1,200 m apart, were selected. Males in both of these colonies were tested with a recording of a series of 11 territorial calls from one male lasting 80 seconds. The loudspeaker was placed 5 m from the male being tested. During the playback all reactions (vocal and behavioral) were noted. Males holding territories on the same beach as the recorded male were noted as "Neighboring Males" and males from the other beach as "Strange Males."

Playback experiments on females and pups were carried out when the pups were 30 to 65 days old. Again, the loudspeaker was placed 5 m from the animal being tested, and reactions were noted during the whole duration of the playback. Each animal was tested with no more than three recordings over a period of 4 days to avoid any habituation. Females were tested soon after their arrival ashore after a feeding trip at sea but before they had located their pups. These tests consisted of playbacks of eight female attraction calls from their own pups and, as a control, eight female attraction calls from other pups. Similarly, the pups were tested at least 24 hours after the departure of their mothers; the tests consisted of playbacks of eight pup attraction calls from their mothers and, as a control, a series of those from other females.

RESULTS

Description and nomenclature of calls

Territorial call (TC)—The territorial call (TC) is a long-distance undirectional vocalization characteristic of adult territorial males, i.e., limited to the breeding season from November to April. This call is emitted in a posture similar to the howling posture of canids, i.e., with head and neck oriented upward or upward and forward. It is emitted spontaneously or in response to other male vocalizations and particularly other TCs. Different authors working on various species of fur seals have described this call as: male roar for *A. tropicalis* (Paulian 1964), high pitched roar for *A. townsendi* (Peterson et al. 1968), trumpeted roar for *C. ursinus* (Peterson 1968), full threat call for *A. forsteri* (Stirling 1971a), male threat call for *A. tropicalis* (Bester 1977), full threat call for *A. australis* (Trillmich and Majluf 1981) and full threat call for *A. townsendi* (Pierson 1987). They are thought to be an advertisement of territorial status (Peterson 1968; Stirling 1971a; Bester 1977; Pierson 1987).

Interindividual variability of TCs was noticed in *A. forsteri* (Stirling 1971a), *A. australis* (Trillmich and Majluf 1981), and *A. townsendi* (Pierson 1987) suggesting that individual recognition, based upon these calls, is possible.

Pup attraction call (PAC)—The pup attraction call (PAC) is a long distance call used by the females when searching for their pups, particularly after returning from a feeding trip at sea. Generally, the females emit this call from the shoreline, in a posture where the neck and the head are oriented upward and forward or directed towards a particular pup calling in the colony. PACs have been described in *C. ursinus* (Bartholomew 1959), *A. tropicalis* (Paulian 1964), *A. gazella* (Bonner 1968), *A. townsendi* (Peterson et al. 1968), *A. forsteri* (Stirling 1971a), *A. pusillus* (Stirling and Warneke 1971), *A. galapagoensis* (Trillmich 1981), and *A. australis* (Trillmich and Majluf 1981). The function of this call in the mother-pup recognition process is obvious and accepted by all these authors.

Female attraction call (FAC)—This high-frequency bleat, characteristic of pups, is principally used in response to a PAC by hungry pups searching for their mothers. This call is utilized during the whole lactation period. Like the PAC, the female attraction call and its role are known for all the fur seal species and have been described as: tremulous bleating for *A. tropicalis* (Paulian 1964), penetrating bleating for *A. gazella* (Bonner 1968), bawl (pup response) for *C. ursinus* (Peterson 1968), female attraction call for *A. forsteri* (Stirling 1971a; McNab and Crawley 1975), female attraction call for *A. tropicalis* (Bester 1977), female attraction call for *A. galapagoensis* (Trillmich 1981), female attraction call for *A. australis* (Trillmich and Majluf 1981), and female attraction call for *A. townsendi* (Pierson 1987).

For *A. tropicalis* (probably as well as the other species), it seems that the main function of this call is not to attract the female (since it is usually the pup who moves towards the calling female) but rather to respond to a PAC, inciting the mother to emit another PAC. A similar process has been described in *Zalophus californianus*, and the pup's call was described as mother response call (Peterson and Bartholomew 1969).

Other calls and postures—For the other calls noted during the experiments: (threat call ThC; male bark or wickering Wic), as well as for the postures (Full Neck Display FND; Open Mouth Display OM; Alert Posture AP), we followed the nomenclature of Stirling (1971a,b).

Individual recognition between territorial males

The playback experiments were performed on 32 different territorial males (15 neighboring males and 17 strange males), all of which reacted to the playback. Of these, 23 males (14 neighboring and 9 strange) responded only to the tape. The others were involved in an interaction with one or more of their neighbors during the playback.

In response to the playbacks, during the experiments the territorial males used seven identified vocalizations or postures: alert posture (AP), open mouth display (OM), threat call (ThC), bark (Wic), full neck display (FND), territorial call (TC), and movement (Mov). The analysis of the responses of the 23 males that responded only to the playbacks (Fig. 1) shows that the neighboring males utilized significantly fewer items of the repertoire ($\bar{x}=2.3$, SD=1.64) than strange males ($\bar{x}=5.1$, SD=0.78, $P\leq 0.001$). A male responds less to the TCs of a neighbor than to those of a strange male, the difference being particularly noticeable in the agonistic reactions (threat calls, open mouth displays, and movements; Fig. 1). This result proves that a territorial male is able to discriminate between the TCs of one of its neighbors and the TCs of a strange male and that some kind of habituation takes place between the neighbors.

Although the responses of the males that were involved in an interaction with another animal during the experiment are more difficult to analyze and are not comparable, it is interesting to note that strange males (who tend to respond more to the playback and more aggressively) were more often involved in a boundary display during the playback (8 out of 17) than neighboring males (1 out of 15).

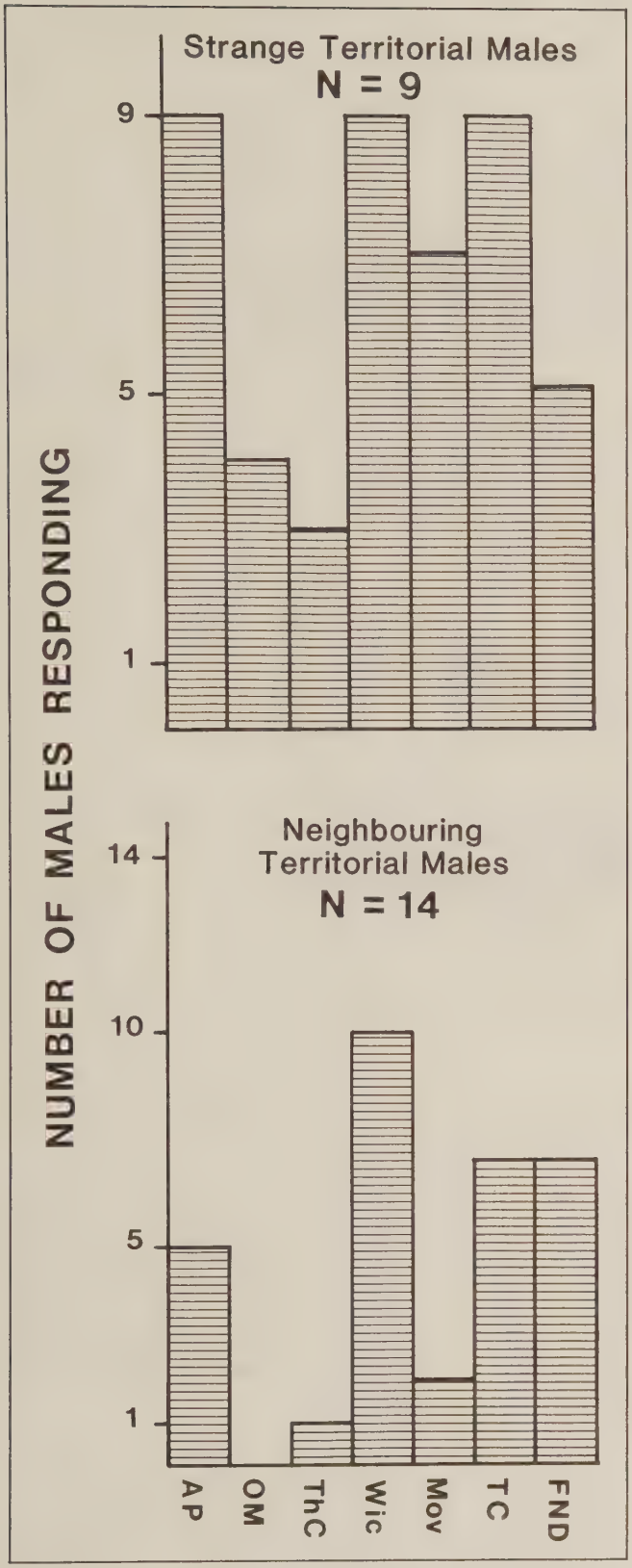


Figure 1—Responses from territorial males to a playback of 11 territorial calls.

To measure TC interindividual variability on sonograms (Fig. 2), the duration (D) and the two frequencies of highest amplitude (F1 and F2) of 4 to 16 TCs from 5 different males were compared pairwise. At least one out of these three measurements was significantly different for each of the 10 different pair combinations (Table 1). The three parameters studied here represent, in fact, only a very small part of the TC interindividual variability, as the structure of the call (particularly the pattern at the beginning and the end of the calls) also clearly separates the different individuals (Fig. 2). These differences provide a sufficient physical basis for individual recognition of the TCs.

Individual recognition between females and pups

When a female returns from a feeding trip at sea, she usually starts calling (PAC) soon after hauling out. Generally, several tens to several hundreds of pups are present within her calling range but only a few respond. The females are quite aggressive towards pups, and the pups are quite reluctant to approach just any female. Before the reunion, the female and her pup always exchange vocalizations. In most cases the first pup to join a given female is actually her own pup. During this study all the marked pups were seen suckling only their mother (N=92). These observations suggest that a long-range mutual recognition system does exist between the females and their pups.

Females are able to locate their respective pups (when they vocalize) without seeing them (behind or under rocks, in caves or crevices). Furthermore, the appearance of the pup is quite variable during the nursing period (wet, dry, muddy, molting, etc.) and artificial changes (coloring) do not affect the female's recognition ability. Pups do not seem to use visual criteria when moving towards their mothers. Hence, if the female discontinues her PACs when the pup is still far away (10 m or more), it is generally unable to locate its mother and wanders around sniffing rocks, other pups or females, and even adult males or human observers. Thus, visual cues do not seem to play any significant role in the mutual recognition process between females and pups.

Olfactory signals certainly play a role, but only at close range (a female is able to discriminate between a strange pup and her own after nuzzling, when two silent pups are presented to her: N=4). But olfactory recognition does not seem to be a prerequisite since some retrievals take place without the traditional nuzzling (five cases). Furthermore, it is possible to inhibit the nuzzling behavior (by spraying the pup's head and back with eau de cologne) without affecting the acceptance of the pup by its mother as long as it is vocalizing (N=10).

When a female started calling after hauling out on the study colony, four pups responded to at least one of her five first PACs ($\bar{x}$=4.1, SD=1.3, N=10), but only one or two pups actually moved towards the calling female ($\bar{x}$=1.5, SD=1.4, N=10). The difference between the number of pups responding to a given female and the number of pups moving towards her is highly significant and shows that during this first phase a selection occurs.

The results of the playback experiments on females are presented in Figure 3. All the females tested with their own pups' vocalizations responded with PACs (N=32), while none of those tested with strange pups' FACs responded (N=15). Thus, females recognize their own pups' vocalizations.

All the pups responded when tested with a playback of their mothers' PACs (N=9), while most of them did not respond when tested with PACs from a strange female (Fig. 4). Pups tested with their mother's PACs responded with significantly more FACs

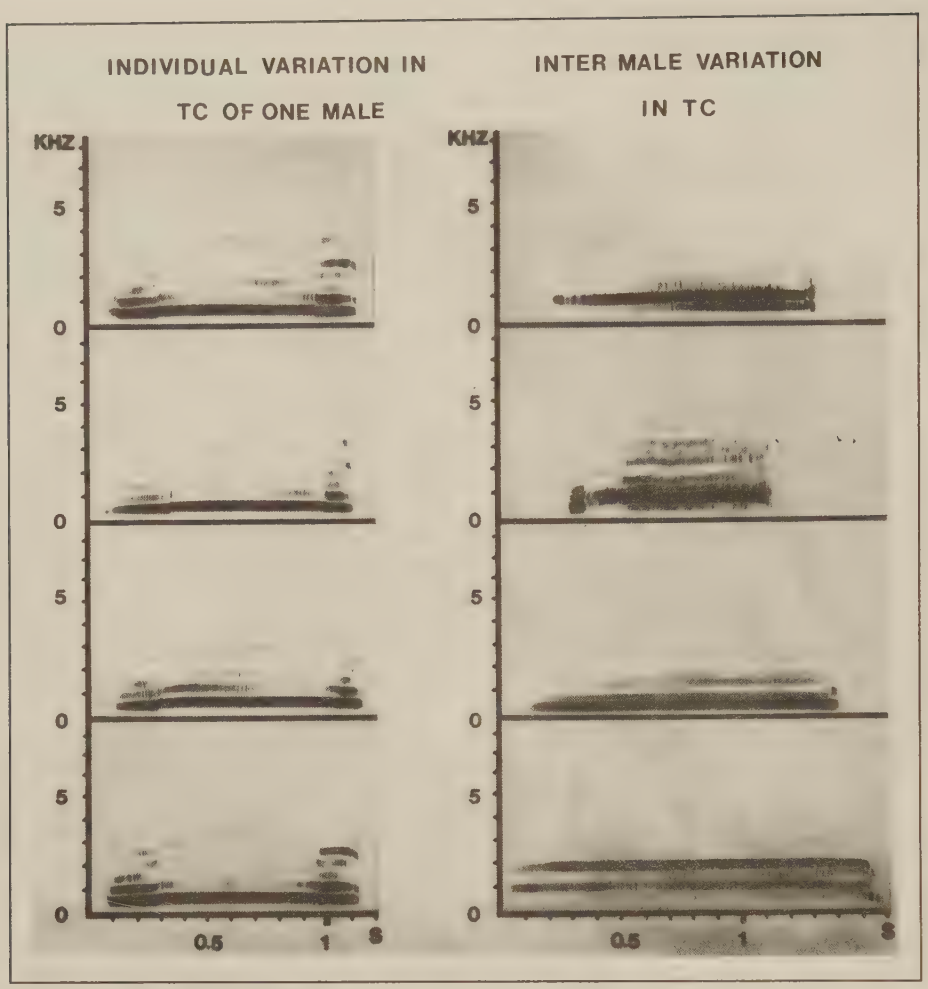


Figure 2—Comparison of sonograms of the territorial calls (TC) from five different males: left, four TCs from the same male; right, four TCs from four different males.

Table 1—Pair-wise comparison of the distinctiveness of territorial calls from five different males. The three measured parameters are the duration of the call (D), and the two frequencies of highest amplitude (F1 and F2). Significance level (S) when $P \leq 0.01$ (t-test).

Male		VI	III	F	VII
	D	ns	S	ns	ns
A	F1	S	S	S	S
	F2	—	S	S	S
	D		S	ns	ns
VI	F1		ns	S	S
	F2		—	—	—
	D			S	ns
III	F1			ns	S
	F2			S	S
	D				ns
F	F1				S
	F2				ns

($\bar{x}$=3.7, SD=0.8) than pups tested with another female's PACs ($\bar{x}$=0.3, SD=0.5, $P<0.001$).

Interindividual variability of PACs and FACs have been investigated in the same way as for the TCs of the males (Figs. 5, 6; Tables 2, 3). Measurements were taken of the sonograms from 32 PACs of five different females and 40 FACs of five different pups. As was the case for TCs, we can conclude that the interindividual variability of both PACs and FACs provide a sufficient physical basis for individual recognition by the pup and the mother, respectively (although 1 out of the 10 different PACs pair combinations did not show any significant difference; Table 2).

DISCUSSION

As with other *Arctocephalus* species (Gentry 1975; McCann 1980), the frequency of fights and boundary displays between two neighboring territorial males decreases significantly a few days after the establishment of the neighbor pair, suggesting that some kind of habituation takes place. During this period of territorial establishment, *A. tropicalis* males utilize territorial calls the most. The interindividual variability of TCs permits individual recognition between males, and even human observers are usually able to distinguish between the TCs of different males. The playback experiments show that a

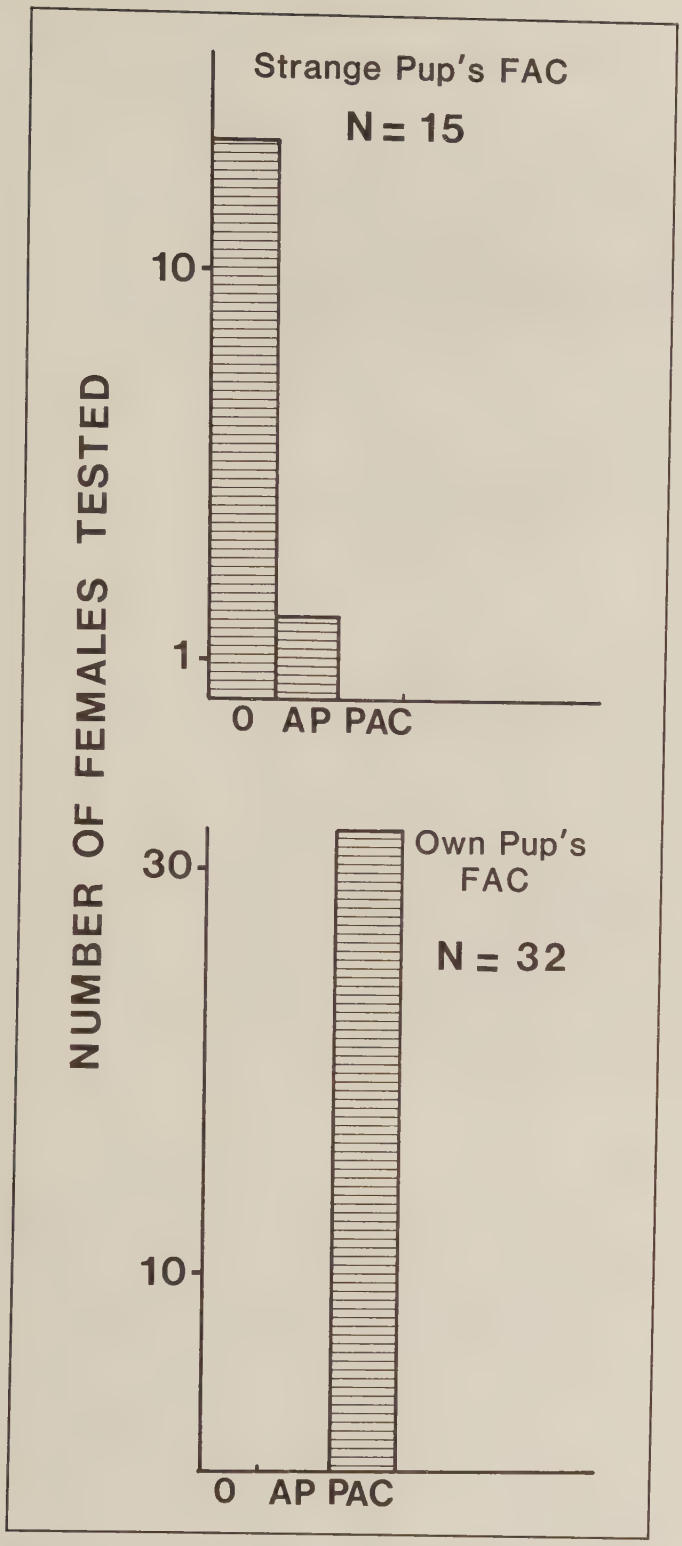


Figure 3—Responses from adult females to a playback of eight female attraction calls (FAC): 0 = no responses; AP = alert posture only; PAC = pup attraction call(s).

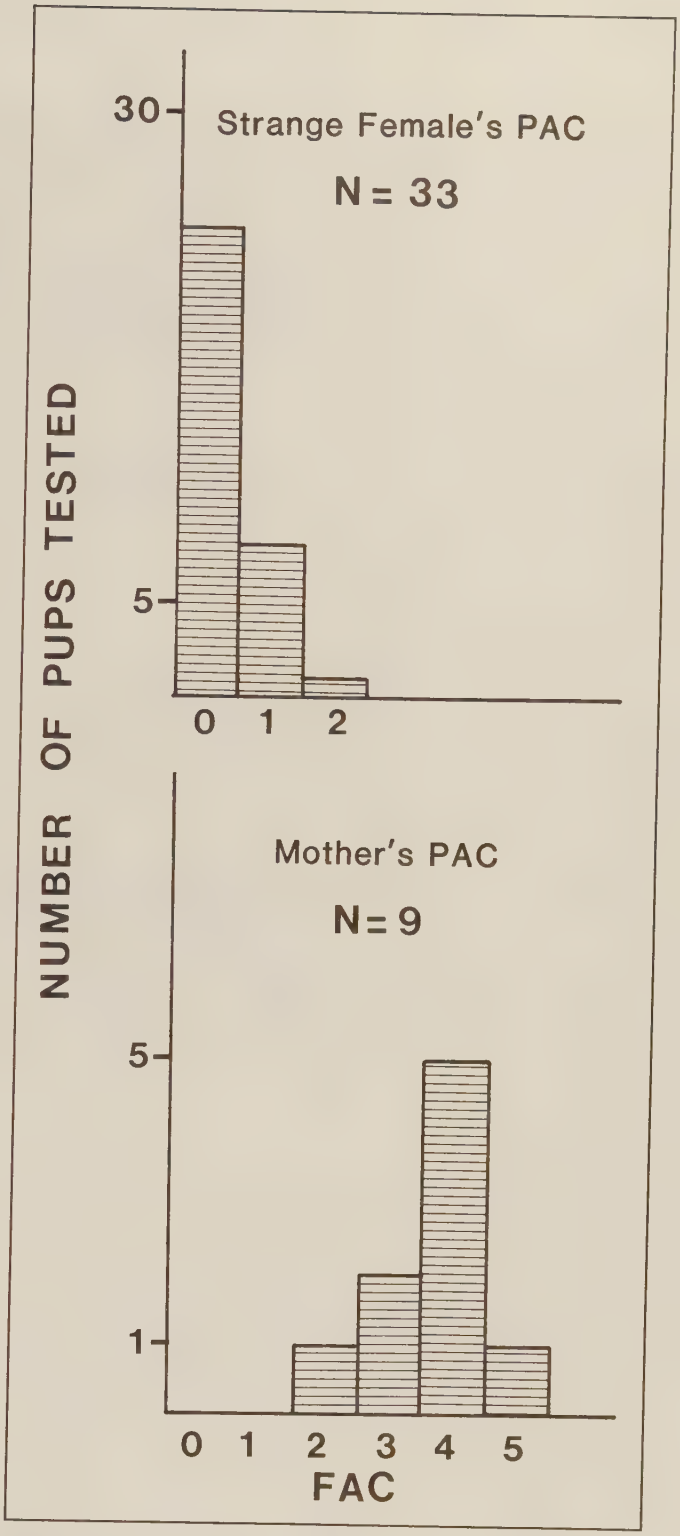


Figure 4—Responses from pups to a playback of eight pup attraction calls.

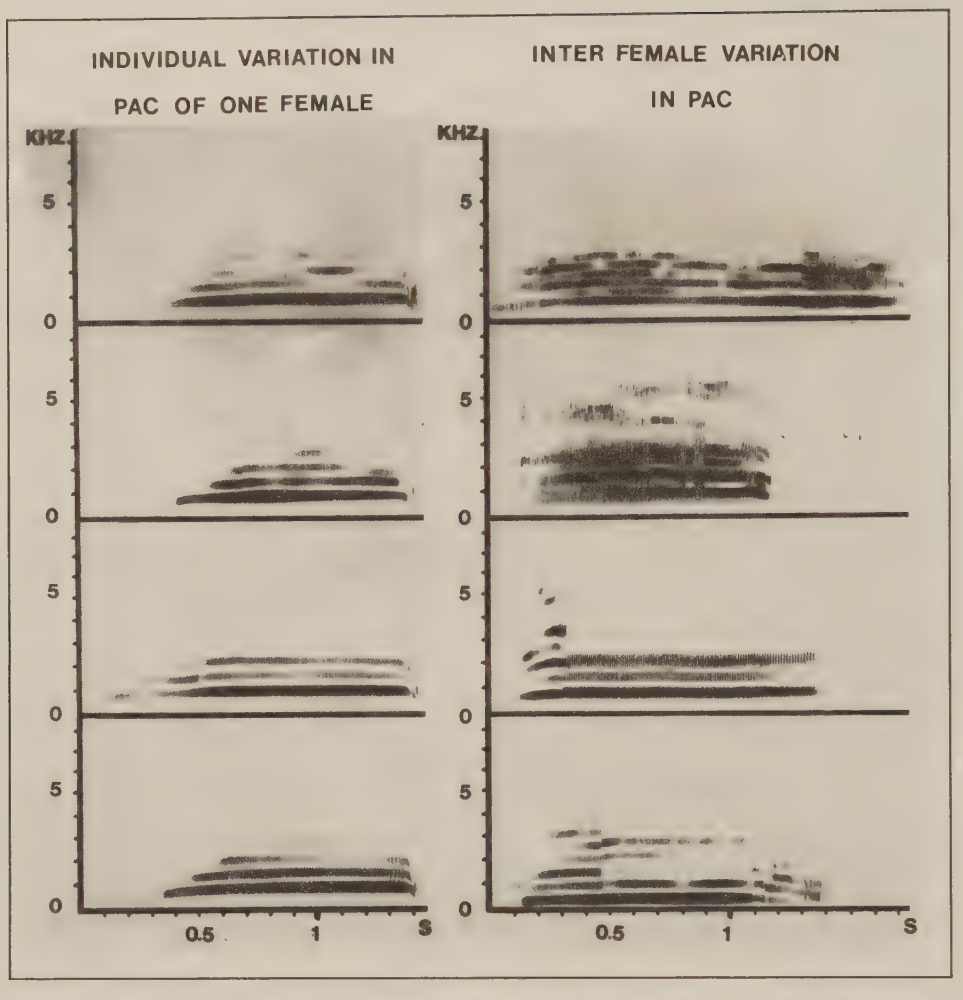


Figure 5—Comparison of sonograms of the pup attraction calls from five different females: left, four PACs from the same female; right, four PACs from four different females.

territorial male is able to discriminate between the vocalizations of a neighbor and those of an unknown male. Furthermore, for established neighbor pairs, a given male reacts less and less aggressively toward one of its neighbor's vocalizations than toward those of a strange male. Thus individual recognition, based upon TCs, contributes to the establishment of the observed habituation even on a very rugged terrain where the other possible cues (visual, olfactory) would be inoperative. Interestingly, of all *Arctocephalus* species the only ones known to use TCs are precisely those breeding generally on rugged terrain, i.e., *A. tropicalis* (this study), *A. forsteri* (Stirling 1971a), and *A. townsendi* (Pierson 1987), as opposed to *A. pusillus* and *A. gazella* (Stirling and Warneke 1971) which generally breed on more open beaches and do not utilize such calls. Since habituation between neighbors occurs in such species as well (McCann 1980), other cues to individual recognition (visual, olfactory) must be utilized by these males.

While feeding at sea, the females are absent from the island for several days. The pups are quite sedentary in the colony where they were born, although some do disperse. (Marked pups, 2.5 months old, have been seen 1 to 3 km away from their birth sites and then seen again a few days later back in their original colony with their mother.) In addition, the actual site where the mother and her pup reunite remains relatively constant for each female-pup pair. So, as was suggested for *C. ursinus* (Peterson 1968), it seems likely that the primary orientation for the mother to reunite with her pup (and for the pup to find its mother) must be geographical. Thereafter, the vocalizations (PACs and FACs) play the most important role in the mutual recognition system between the female and her pup; hence vocalizing is the only prerequisite to any reunion between a mother and her pup.

As suggested for most species, the females recognize their pups' FACs, and as has been shown in *A. galapagoensis* (Trillmich 1981), *A. tropicalis* pups also recognize their mothers' vocalizations (PACs). The pups' ability to recognize their mothers' vocalizations is less selective than the females' discriminating ability during the playback experiments (females only responded to their own pup's FACS; Figs. 3 and 4). This is consistent with the observations of more than one pup ($\bar{x}=4$) initially responding to any given female calling in the colony. Therefore, the mother takes a more active part in the auditory mutual recognition process than the pup.

The calls emitted by adult females and males which carry identity information (PACs and TCs, respectively) show striking structural similarities; a large overlap exists for all the measurements on the sonograms (Fig. 7). The posture in which females and males emit these calls is also similar. Although the functions of these calls are quite different, all the affinities suggest that PACs and TCs are,

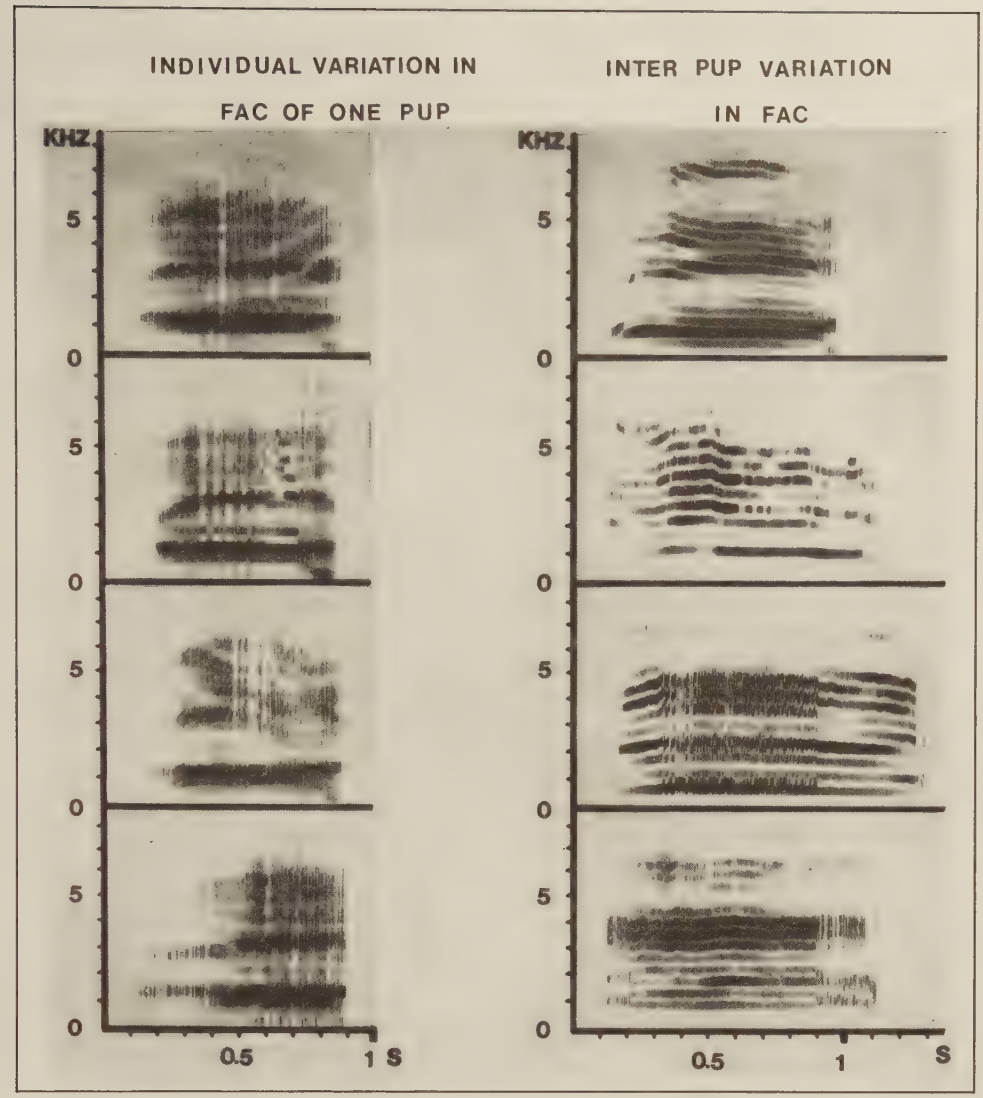


Figure 6—Comparison of sonograms of the female attraction calls from five different pups: left, four FACs from the same pup; right, four FACs from four different pups.

Table 2—Pair-wise comparison of the distinctiveness of pup attraction calls from five different females. Significance level (S) when $P \leq 0.01$ (t-test). D = duration of call; F1 and F2 = two frequencies of highest amplitude.

Female		G	S	U	Z
	D	ns	ns	S	ns
115	F1	S	S	S	ns
	F2	S	ns	S	ns
	D		S	ns	S
G	F1		S	ns	S
	F2		S	S	S
	D			S	ns
S	F1			S	S
	F2			S	ns
	D				S
U	F1				S
	F2				S

Table 3—Pair-wise comparison of the distinctiveness of female attraction calls from five different pups. Significance level (S) when $P \leq 0.01$ (t-test). D = duration of call; F1 and F2 = two frequencies of highest amplitude.

Pup		B	Y	85	K
	D	S	S	ns	ns
AL	F1	S	S	S	S
	F2	S	S	ns	S
	D		S	ns	ns
B	F1		S	S	S
	F2		S	S	S
	D			ns	ns
Y	F1			S	S
	F2			ns	ns
	D				ns
85	F1				S
	F2				S

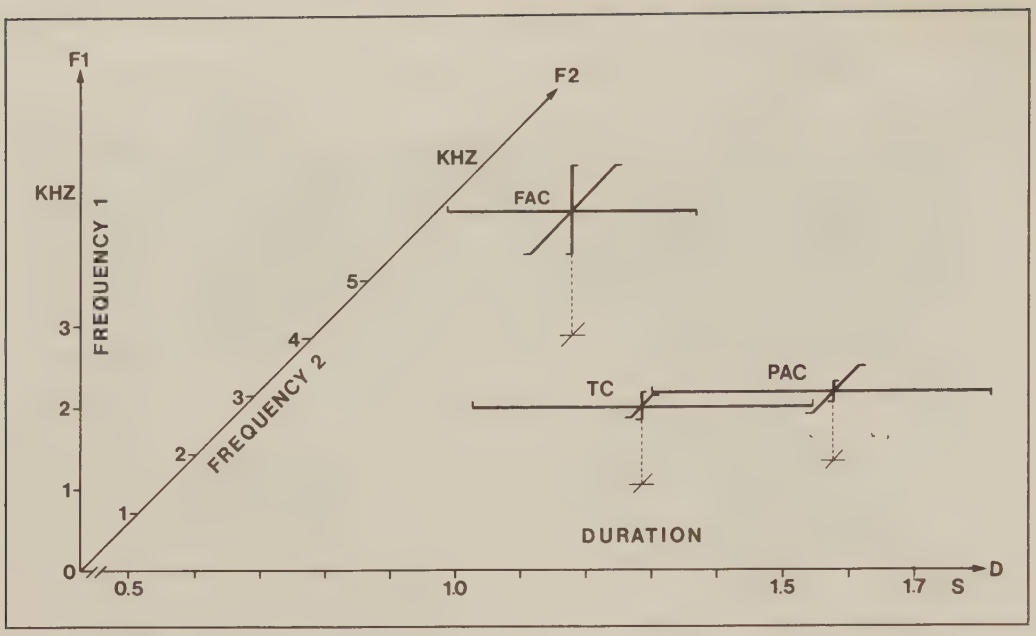


Figure 7—Variability of the three calls supporting individual recognition according to the three parameters measured on the sonograms (Mean ±SD): TC = 40 calls from 5 different males; PAC = 38 calls from 9 different females; FAC = 45 calls from 10 different pups.

in fact, analogous calls used by the two sexes. These two calls, which carry identity information, are utilized by the males as territorial calls (allowing habituation between the neighbors) and as pup attraction calls by the females (permitting individual recognition by their pups).

ACKNOWLEDGMENTS

This work was a contribution to the program "Ecologie des Oiseaux et Mammifères Antarctiques" (Ecology of Antarctic birds and mammals) of Terres Australes et Antarctiques Francaises (TAAF) and Recherche Coordonnée sur Programme 764 of Centre National de la Recherche Scientifique. We would like to express our sincere thanks to the 32nd and 33rd relief teams to Amsterdam Island for their hospitality, to TAAF administration for financial and logistic support, and I. Stirling for kindly reviewing the manuscript.

CITATIONS

BARTHOLOMEW, G. A.
1959. Mother-young relations and the maturation of pup behaviour in the Alaska fur seal. Anim. Behav. 7:163-171.

BESTER, M. N.
1977. Habitat selection, seasonal population changes and behaviour of the Amsterdam Island fur seal *Arctocephalus tropicalis*, on Gough Island. D.Sc. Thesis, Univ. Pretoria, R.S.A., 193 p.

BONNER, W. N.
1968. The fur seal of South Georgia. Br. Antarct. Surv. Sci. Rep. 56, 93 p.

GENTRY, R. L.
1975. Comparative social behaviour of eared seals. Rapp. P-v. Reun. Cons. Int. Explor. Mer 169:189-194.

HES, A. D., and J-P. ROUX.
1983. Population increase in the subantarctic fur seal, *Arctocephalus tropicalis*, at Amsterdam Island. S. Afr. J. Antarct. Res. 13:29-34.

McCANN, T. S.
1980. Territoriality and breeding behaviour of adult males antarctic fur seals, *Arctocephalus gazella*. J. Zool. (Lond.) 192:295-310.

McNAB, A. G., and M. C. CRAWLEY.
1975. Mother and pup behaviour of the New Zealand fur seal, *Arctocephalus forsteri* (Lesson). Mauri Ora 3:77-88.

PAULIAN, P.
1964. Contribution à l'étude de l'Otarie de l'île Amsterdam (A contribution to the study of the Amsterdam Island fur seal). Mammalia 28(1):1-146.

PETERSON, R. S.
1968. Social behavior in pinnipeds. *In* Harrison, R. J., et al. (eds.), The behavior and physiology of Pinnipeds, p. 3-53. Appleton Century Crofts, New York.

PETERSON, R. S., and G. A. BARTHOLOMEW.
1969. Airborne vocal communications in the California sea lion, *Zalophus californianus*. Anim. Behav. 17:17-24.

PETERSON, R. S., C. L. HUBBS, R. L. GENTRY, and R. L. DeLONG.
1968. The Guadalupe fur seal: habitat, behaviour, population size and field identification. J. Mammal. 49:665-675.

PIERSON, M. O.
1987. Breeding behavior of the Guadalupe fur seal, *Arctocephalus townsendi*. *In* Croxall, J. P., and R. L. Gentry (eds.), Status, biology, and ecology of fur seals, p. 83-94. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 51.

ROUX, J-P.
1982. L'Otarie d'Amsterdam (The Amsterdam Island fur seal). Actes 6e Colloq. Mammal., La Rochelle, p. 75-79.
1987. Recolonization processes in the subantarctic fur seal, *Arctocephalus tropicalis*, on Amsterdam Island. *In* Croxall, J. P., and R. L. Gentry (eds.), Status, biology, and ecology of fur seals, p. 189-194. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 51.

ROUX, J-P., and A. D. HES.
1984. The seasonal haul-out cycle of the fur seal *Arctocephalus tropicalis* (Gray, 1872) on Amsterdam Island. Mammalia 48(3):377-389.

STIRLING, I.
1971a. Studies on the behaviour of the South Australian fur seal, *Arctocephalus forsteri* (Lesson). 1. Annual cycle, postures and calls and adult males during the breeding season. Aust. J. Zool. 19:243-266.
1971b. Studies on the behaviour of the South Australian fur seal, *Arctocephalus forsteri* (Lesson). 2. Adult females and pups. Aust. J. Zool. 19:267-273.

STIRLING, I., and R. M. WARNEKE.
1971. Implications of a comparison of the airborne vocalizations and some aspects of the behaviour of the two Australian fur seals, *Arctocephalus* spp, on the evolution and present taxonomy of the genus. Aust. J. Zool. 19:227-241.

TRILLMICH, F.
1981. Mutual mother-pup recognition in Galapagos fur seals and sea lions: cues used and functional significance. Behaviour 78:21-42.

TRILLMICH, F., and P. MAJLUF.
1981. First observations on colony structure, behaviour, and vocal repertoire of the South American fur seal (*Arctocephalus australis* Zimmerman, 1783) in Peru. Z. Saugetierkunde 46:310-322.

Interactions Between Guadalupe Fur Seals and California Sea Lions at San Nicolas and San Miguel Islands, California

BRENT S. STEWART
Hubbs Marine Research Center
1700 South Shores Rd.
San Diego, California 92109

PAMELA K. YOCHEM
Hubbs Marine Research Center
1700 South Shores Rd.
San Diego, California 92109

ROBERT L. DeLONG
National Marine Mammal Laboratory
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE, Bldg. 4
Seattle, Washington 98115

GEORGE A. ANTONELIS, JR.
National Marine Mammal Laboratory
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE, Bldg. 4
Seattle, Washington 98115

ABSTRACT

Sightings of adult and juvenile Guadalupe fur seals, *Arctocephalus townsendi*, at some of the Southern California Channel Islands have become more common during the past decade. Since 1969 we have made 43 sightings of Guadalupe fur seals, primarily of subadult and adult males, at San Nicolas and San Miguel Islands. One adult *A. townsendi* was present at San Nicolas Island each summer from 1981 through 1986. He defended a territory among breeding California sea lions and attempted to herd and mount the females; he successfully mounted three females, and intromission apparently occurred once. In each interspecific interaction observed, adult Guadalupe fur seals appeared to be socially dominant to California sea lions. These observations suggest that Guadalupe fur seals are likely to be successful in obtaining space for breeding among California sea lions on the Southern California Channel Islands. Reestablishment of a breeding population in the Southern California Bight may therefore depend primarily on a continued increase in abundance of Guadalupe fur seals in U.S. waters. This increase in abundance will, however, ultimately depend on the continued growth of the population at the species' sole colony in Mexican waters at Isla de Guadalupe.

INTRODUCTION AND METHODS

The Guadalupe fur seal, *Arctocephalus townsendi*, apparently ranged historically from Isla Revillagigedo northward to Point Conception, California (Morrell 1832; Townsend 1899; Starks 1922; Lyon 1937; Repenning et al. 1971), and archaeological evidence suggests that Guadalupe fur seals may have been abundant at San Miguel Island (lat. 34°02′N., long. 120°22′W; Walker and Craig 1979). Other than the interesting report of "three Guadalupe fur seal bulls" at Piedras Blancas in 1938 (Bonnot et al. 1938; Bonnot 1951), the only confirmed records of Guadalupe fur seals north of Point Conception are two recent strandings (Roletto 1984; Webber in press).

Guadalupe fur seals were harvested commercially for their pelts off the coasts of Alta and Baja California by sealers and sea otter, *Enhydra lutris*, hunters from the late 1700s through the late 1800s (Morrell 1832; Townsend 1899; Odgen 1941; Hubbs 1956; Busch 1985). The last recorded commercial catch was in 1894 at Isla de Guadalupe, and the species was believed to be extinct in 1897 (Hubbs 1956). It reappeared briefly in the 1920s (Hubbs 1956), but confirmed sightings were not reported again until 1949 when a subadult male was seen at San Nicolas Island (lat. 33°15′N, long. 119°30′W; Bartholomew 1950). Subsequent expeditions to historical rookeries on the islands off Baja California found a small breeding colony at Isla de Guadalupe (Hubbs 1956), and this apparently remains the only location where breeding occurs. Coincident with a modest increase in that population (Huey 1930; Townsend 1930; Peterson et al. 1968b; Fleischer 1978) has been an increase in sightings of Guadalupe fur seals in U.S. waters (Table 1).

We have recorded the presence of Guadalupe fur seals each summer at San Miguel Island since 1969 (DeLong and Antonelis) and during weekly to monthly censuses of pinniped populations (Stewart and Yochem 1984) at San Nicolas Island since 1980. We have photographed several of these fur seals, especially those with distinct scars, to permit reidentification. We made incidental observations of the behavior of fur seals during our studies of behavior and population dynamics of other pinniped species.

Here we summarize recent records of *A. townsendi* in U.S. waters and report our observations of Guadalupe fur seals and of their interactions with California sea lions, *Zalophus californianus*, at San Nicolas and San Miguel islands.

RESULTS

We have made 43 sightings of Guadalupe fur seals at San Nicolas and San Miguel Islands since 1969 (Table 1); nearly all were of subadult (37%) and adult (34%) males. At least two fur seals were seen in more than 1 year; at San Nicolas Island, an adult female was present in 1983 and 1984, and an adult male (described below) was present in 6 consecutive years.

In summer 1981, an adult male Guadalupe fur seal maintained a territory among breeding California sea lions at San Nicolas Island for about 35 days (Stewart 1981). We observed this male (identified by flipper and body scars) again each summer through 1986 at the island where he defended the same area. He was present for about 122 days in 1982, at least 105 days in 1983, and 46 days in 1984. We observed this fur seal for a total of about 35 hours. He was inactive (lying down, either sleeping or resting), for an average of 95% (56.6 ± 3.1 min) of each hour of observation. He spent the remaining time either patroling his territory (1.2 ± 1.2 min/hr) or interacting with sea lions (1.8 ± 1.2 min/h). Of 87 inter-

Table 1—Summary of recent sightings of *Arctocephalus townsendi* in U.S. waters.

Date	Location	Sex and relative age	Source
12 May-July 1949	San Nicolas I.	Adult male	Bartholomew 1950, 1951
17 Nov. 1967	Lat. 33°30′N, Long. 122°00′W	Adult male (at sea)	Brownell and DeLong 1968
17 Feb. 1968	San Miguel I.	Subadult male	Peterson et al. 1968a
24 Aug. 1968	San Miguel I.	Adult male	Peterson and LeBoeuf 1969
31 Aug. 1968	San Miguel I.	Juvenile male or female	Peterson and LeBoeuf 1969
May-Sept. 1969	San Miguel I.	Adult male, subadult male	This report
Aug. 1970	San Miguel I.	Adult male	This report
31 Aug. 1971	San Miguel I.	Adult male, subadult male, juvenile female	This report
Sept. 1971	San Miguel I.	Juvenile female	This report
Aug. 1972	San Miguel I.	2 Adult males	This report
Aug. 1973	San Miguel I.	Adult male, subadult male	This report
27 June 1975	San Miguel I.	Subadult male	Bonnell et al. 1980
July 1975	San Miguel I.	1 seal	Mate 1977
4 Aug. 1975	San Clemente I.	Juvenile male	Bonnell et al. 1980
20 Aug. 1975	San Miguel I.	Adult male, subadult male	This report
25 Jan. 1976	75 km South of Santa Rosa I.	Adult male (at sea)	Bonnell et al. 1980
25 Jan. 1976	Lat. 31°51′N. Long. 119°41′W	1 seal (at sea)	Bonnell et al. 1980
29 July 1976	San Miguel I.	Adult male, 2 subadult males	This report
25 Apr. 1977	Monterey Bay	Juvenile male (beached)	Webber In press
30 July 1977	San Miguel I.	Adult male, 2 subadult males	This report
19 June 1978	San Miguel I.	Subadult male	This report
4 Aug. 1978	San Miguel I.	4 Juvenile males	This report
2 Sep. 1979	San Miguel I.	Subadult male	This report
Summer 1980	San Miguel I.	Subadult male	P. J. Gearin, pers. commun. Natl. Mar. Mamm. Lab., Seattle
4 July 1981	San Nicolas I.	Juvenile	Stewart 1981
26 June-1 Aug. 1981	San Nicolas I.	Adult male	Stewart 1981
13 Aug. 1981	San Miguel I.	2 Juveniles	This report
26 May-1 Oct. 1982	San Nicolas I.	Adult male	This report
28 June 1982	San Nicolas I.	Juvenile	J. Francis, pers. commun., Univ. Calif., Santa Cruz
3 July 1982	San Nicolas I.	Juvenile	C. Heath, pers. commun., Univ. Calif., Santa Cruz
10 July 1982	San Nicolas I.	Juvenile	This report
14 July 1982	San Nicolas I.	Juvenile	C. Heath, pers. commun., Univ. Calif., Santa Cruz
26 July 1982	San Nicolas I.	Juvenile	J. Francis, pers. commun., Univ. Calif., Santa Cruz
28 July 1982	Santa Barbara I.	Juvenile	J. Francis, pers. commun., Univ. Calif., Santa Cruz
31 July 1982	Santa Barbara I.	Juvenile	J. Francis, pers. commun., Univ. Calif., Santa Cruz
1 Oct. 1982	San Nicolas I.	Juvenile	Stewart and Yochem 1984
10 Oct. 1982	San Miguel I.	Subadult male	This report
17 April 1983	San Nicolas I.	Juvenile male	C. Heath, pers. commun., Univ. Calif., Santa Cruz
1 May 1983	San Nicolas I.	Juvenile	This report
22 May-5 Sept. 1983	San Nicolas I.	Adult male	This report
17 July 1983	San Nicolas I.	Adult female	This report
28 July 1983	San Miguel I.	Adult male, 2 subadult males	This report
5 Feb. 1984	San Miguel I.	Juvenile male or adult female	This report
18 May 1984	San Mateo Co.	Juvenile female (beached alive)	Roletto 1984
1 June (16 July) 1984[a]	San Nicolas I.	Adult male	This report
19-26 May, 10-16 June 1984	San Nicolas I.	Adult female	This report
2 Aug. 1984	San Miguel I.	Subadult male	This report
5 Feb. 1985	San Miguel I.	Juvenile male or adult female	This report
Summer 1985[b]	San Nicolas I.	Adult male	This report
23 May 1986/summer	San Nicolas I.	Adult male	This report
28 July 1986	San Miguel I.	Subadult male	Gearin and Antonelis 1986

[a]The seal was present up through 16 July when we ended our field season. He may have been present during August but had departed prior to 15 September when we conducted a census.

[b]Surveys were also conducted at San Miguel Island in summer 1985 but no Guadalupe fur seals were seen (Stewart 1985).

actions observed, 45 (52%) were with female sea lions. During these interactions the male approached and either attempted to herd a female that was moving out of or through his territory (89% of all interactions) or sniffed at the female's muzzle or urogenital region (11%). In general, females responded by vocally threatening the male (7%), retreating and escaping from his territory (13%), passively remaining in the territory (56%), or resisting the male's herding attempts initially before submitting and remaining in his territory (24%). We observed physical contact, or evidence of contact (Stewart 1981), seven times between the fur seal and female sea lions. Twice in 1983, and once in 1984, the male mounted and attempted to copulate with sea lion females; intromission apparently occurred during at least one of these attempts (pelvic thrusts were observed) and lasted approximately 5 minutes.

Of 42 interactions observed between the male fur seal and male sea lions, 24 (57%) were with subadults and 18 (43%) were with nearby territorial adults. Preceding each encounter the fur seal approached (while vocalizing) a male sea lion that was either passing through his territory or vocalizing nearby. When physical contact did not occur (90% of all interactions) each sea lion male retreated

as the fur seal approached. We observed physical contact between the fur seal and sea lion males four times: once with an adult and three times with subadults. Physical interactions were brief (less than 30 seconds), and the sea lion males retreated in each case. In early June 1984 we observed several fresh wounds on the fur seal's neck. We presume that these were inflicted by an adult sea lion male (which was subsequently displaced) rather than by a female sea lion.

Two juvenile fur seals (sex undetermined, one in 1981 and one in 1982) were ashore briefly within 100 m of the adult male fur seal, but we did not observe them to interact either with the male or with California sea lions.

An adult female Gaudalupe fur seal was present at San Nicolas Island in summer 1983 and in 1984 (same female, identified by scars; Table 1). She was never observed to be closer than about 0.5 km to the male fur seal. In the single interaction observed between this female and California sea lions, two female sea lions were simultaneously displaced after being threatened vocally by the fur seal.

In February 1984, Stewart observed and photographed a Guadalupe fur seal at San Miguel Island. A juvenile sea lion that approached to within 1 m of the fur seal was vocally threatened and chased away. From its behavior, size, and apparent lack of a penile opening, this fur seal appeared to be an adult female; however, we were unable to confirm its sex later from photographs. Antonelis observed similar behavior during interactions between subadult male Guadalupe fur seals and California sea lion females at San Miguel Island. The presence of a penile opening in young fur seals is often difficult to confirm because of its small size and concealment by the thick fur coat. Testicles of sexually immature males are often undetectable. The fur seal that we observed may, therefore, have been a juvenile male rather than an adult female.

In June 1976, Antonelis observed an adult male *A. townsendi* at San Miguel Island exhibit territorial behavior similar to that described above for the male at San Nicolas Island. This male attempted to herd California sea lion females and pups, and he repeatedly picked up one dead sea lion pup by the neck and carried it to several areas at or near the boundaries of his territory. Once, the fur seal laid this pup on a flat rock, mounted it, and attempted to copulate with it for about one minute. Although the death of the pup was not witnessed, the freshness of the carcass and the behavior of the male toward it suggest that the pup might have died as a result of the copulatory efforts of the male.

DISCUSSION

Our limited observations suggest that adult male and female Guadalupe fur seals are socially dominant to adult sea lions when ashore and are able to exclude sea lions from areas during the summer breeding season. This is consistent with observations by DeLong (1982) and Bonnell et al. (1980) who reported that *A. townsendi* males were successful in maintaining territories among sea lions at San Miguel Island. In summer 1973, at San Miguel Island, a male Guadalupe fur seal completely excluded California sea lions from a territory that he had apparently established by displacing them (DeLong 1982). On three other occasions, however, subadult male fur seals were displaced by adult California sea lions as the fur seals moved toward or within groups of sea lion females (DeLong 1982). It is possible that the areas from which sea lions are apparently excluded by Guadalupe fur seals are actually marginal or lesser preferred hauling or rookery areas for California sea lions. At Isla de Guadalupe, Guadalupe fur seals haul out on solid rock, bouldered, or cobbled substrate; they are generally spatially segregated from other pinniped species on hauling grounds and rookeries (Berdegue 1957; Peterson et al. 1968b; Fleischer 1978). Peterson et al. (1968b) attributed this segregated distribution to differences in habitat preference, and they briefly considered the influence of interspecific competition on these apparent preferences. With one exception (a subadult male hauled out on a broad sandy beach), all fur seals we observed at San Miguel Island were hauled out on substrate similar to that used at Isla de Guadalupe. The fur seals that we observed at San Nicolas Island were hauled out on flat, low, sandstone terraces very near the surf, with the exception of the adult male who occasionally rested in a sand-bottomed (usually wet) crevasse in the sandstone. Systematic observations of interactions on a variety of substrate or habitat types are needed to determine if Guadalupe fur seals are truly dominant to California sea lions when competing for hauling or breeding space.

Off the coasts of Baja and Alta California, the range of Guadalupe fur seals is sympatric with or overlaps the ranges of California sea lions, harbor seals (*Phoca vitulina*), northern elephant seals (*Mirounga angustirostris*), northern fur seals (*Callorhinus ursinus*), and Steller sea lions (*Eumetopias jubatus*). Populations of each of these species have changed dramatically during the past several decades (Antonelis et al. 1981; DeLong 1982; DeMaster et al. 1982; Cooper and Stewart 1982, 1983; LeBoeuf et al. 1983; Stewart and Yochem 1984; Stewart et al. In press). Although it is likely that interactions among these species at sea and ashore will influence the population dynamics of each, data are inadequate to predict the importance of these interactions in structuring the pinniped community in the Southern California Bight. Steller sea lions have been relatively numerous historically (Bonnot 1951; Bonnell et al. 1980) at San Miguel Island (the southern limit of their range) and have appeared successful in displacing California sea lions (DeLong 1982). The population has, however, declined dramatically (breeding no longer occurs) during the past several decades, but this decline is related to changes in the abundance of the species in California waters, due apparently to factors (Ainley and Lewis 1974) other than the dynamics of interspecific interactions while ashore.

Our behavioral observations suggest that Guadalupe fur seals are capable of obtaining space for breeding among California sea lions and that they may successfully recolonize the Southern California Channel Islands once they are abundant enough to establish a breeding population. The increase in sightings of Guadalupe fur seals at or near the Southern California Channel Islands suggests an increase in abundance (during some seasons) of this species in U.S. waters. Since these incipient colonizers are presumably all derived from the population at Isla de Guadalupe, the most important factor in recolonization of the Southern California Channel Islands will likely be the continued growth of the population at the species' sole colony on Isla de Gaudalupe.

ACKNOWLEDGMENTS

We thank LCDR E. Giffin and R. Dow and his staff for arranging access to San Nicolas Island; W. Ehorn and the staff of the Channel Islands National Park for their support of our work at San Miguel Island; J. Francis, C. Heath, and P. J. Gearin for sharing with us their observations of fur seals at San Nicolas and Santa Barbara Islands and for reviewing an early draft of the manuscript; and J. P. Croxall and L. Fleischer for their review of and comments on the manuscript. We owe a special thanks to D. Day, Scripps Institute

of Oceanography (SIO) archivist, for permitting our access to the Carl Hubbs library collection at SIO and for helping to locate materials used in our review of *A. townsendi*. The work of B. S. Stewart and P. K. Yochem was supported by U.S. Air Force Contract FO4701-81-C-0018 and a research grant from the El Dorado Chapter of the National Audubon Society.

CITATIONS

AINLEY, D. G., and T. G. LEWIS.
1974. The history of Farallon Island marine bird populations, 1854-1972. Condor 76:432-446.

ANTONELIS, G. A., Jr., S. LEATHERWOOD, and D. K. ODELL.
1981. Population growth and censuses of the northern elephant seal, *Mirounga angustirostris*, on the California Channel Islands, 1958-1978. Fish. Bull., U.S. 79:562-567.

BARTHOLOMEW, G. A., Jr.
1950. A male Guadalupe fur seal on San Nicolas Island, California. J. Mammal. 31:175-180.
1951. Spring, summer, and fall censuses of the pinnipeds on San Nicolas Island, California. J. Mammal. 32:15-21.

BERDEGUE, J.
1957. Redescrubrimiento de la foca fina (*Arctocephalus townsendi*, Merriam) en la Isla de Guadalupe, Mexico; con notas acerca de la biologia de otros pinnipedos existentes en esas aguas). Rev. Soc. Mex. Hist. Nat. 18:173-198.

BONNELL, M. L., B. J. LeBOEUF, M. O. PIERSON, D. H. DETTMAN, G. D. FARRENS, C. B. HEATH, R. F. GANTT, and D. J. LARSEN.
1980. Pinnipeds of the Southern California Bight area, 1975-1978. Vol. 3, Part 1. Contract Rep. by Univ. Calif. Santa Cruz for Bureau of Land Management. NTIS PB 81-248-71, 535 p.

BONNOT, P.
1951. The sea lions, seals, and sea otter of the California coast. Calif. Fish Game 37:371-389.

BONNOT, P., G. H. CLARK, and S. R. HATTON.
1938. California sea lion census for 1938. Calif. Fish Game 24:415-419.

BROWNELL, R. L., and R. L. DeLONG.
1968. Marine mammals of the eastern grid area. Unpubl. rep. prepared for Pac. Ocean Biol. Surv. Prog., Smithson. Inst., Wash., D.C., 10 p.

BUSCH, B. C.
1985. The war against the seals: A history of the North American seal fishery in the 19th and 20th centuries. McGill-Queen's Univ. Press, Montreal, 374 p.

COOPER, C. F., and B. S. STEWART.
1982. The perils of success: implications of increasing marine mammal populations in the Southern California Bight. Proc. Ocean Studies Symp., Asilomar, Calif., 7-10 Nov. 1982. Calif. Coastal Comm., San Francisco, 11 p.
1983. Demography of northern elephant seals, 1911-1982. Science 210:969-971.

DeLONG, R. L.
1982. Population biology of northern fur seals at San Miguel Island, California. Ph.D. Thesis, Univ. Calif., Berkeley, 185 p.

DeMASTER, D. P., D. J. MILLER, D. GOODMAN, R. L. DeLONG, and B. S. STEWART.
1982. Assessment of California sea lion-fishery interactions. Trans. N. Am. Wildl. Nat. Resour. Conf. 47:253-264.

FLEISCHER, L. A.
1978. The distribution, abundance and population characteristics of the Guadalupe fur seal, *Arctocephalus townsendi* (Merriam 1897). M.S. Thesis, Univ. Wash., Seattle, 93 p.

GEARIN, P. J., and G. A. ANTONELIS, Jr.
1986. Preliminary results of pinniped studies at San Miguel Island, California, 8 June-31 July 1986. NMFS rep., Natl. Mar. Mammal Lab., Seattle, WA, 25 p.

HUBBS, C. L.
1956. Back from oblivion. Guadalupe fur seal: still a living species. Pac. Discovery. 9:14-21.

HUEY, L. H.
1930. Past and present status of the northern elephant seal with a note on the Guadalupe fur seal. J. Mammal. 11:188-194.

LeBOEUF, B. J., D. AURIOLES, R. CONDIT, C. FOX, R. GISINER, R. ROMERO, and F. SINSEL.
1983. Size and distribution of the California sea lion population in Mexico. Proc. Calif. Acad. Sci. 43:77-85.

LYON, G. M.
1937. Pinnipeds and a sea otter from the Point Mugu shell mound of California. Publ. Univ. Calif. Los Angeles Biol. Sci. 1:133-168.

MATE, B. R.
1977. Aerial censusing of pinnipeds in the eastern Pacific for assessment of population numbers, migratory distributions, rookery stability, breeding effort, and recruitment. Rep. MMC-75/01 to U.S. Mar. Mamm. Comm. by Oreg. State Univ., Newport, 67 p.

MORRELL, B.
1832. A narrative of four voyages to the South Seas, North and South Pacific Oceans, Chinese Sea, Ethiopic and southern Atlantic Ocean, Indian and Antarctic Ocean, from the year 1822 to 1831, comprising critical surveys of coasts and islands with sailing directions and an account of some new and valuable discoveries including the Massacre Islands where 13 of the author's crew were massacred and eaten by cannibals, to which is prefixed a brief sketch of the author's life. J. and J. Harper, New York, 492 p.

OGDEN, A.
1941. The California sea otter trade; 1784-1848. Univ. Calif. Publ. Hist. 26:1-251.

PETERSON, R. S., R. L. GENTRY, and B. J. LeBOEUF.
1968a. Investigations of pinnipeds on San Miguel and San Nicolas islands. Unpubl. rep., Univ. Calif., Santa Cruz, 15 p.

PETERSON, R. S., C. L. HUBBS, R. L. GENTRY, and R. L. DeLONG.
1968b. The Guadalupe fur seal: habitat, behavior, population size and field identification. J. Mammal. 49:665-675.

PETERSON, R. S., and B. J. LeBOEUF.
1969. Fur seals in California. Pac. Discovery. 22:12-15.

REPENNING, C. A., R. S. PETERSON, and C. L. HUBBS.
1971. Contributions to the systematics of the southern fur seals, with particular reference to the Juan Fernandez and Guadalupe species. Antarctic Pinnipedia. Antarct. Res. Ser. 18:1-34.

ROLETTO, J.
1984. The most northernly sighting of a live Guadalupe fur seal, *Arctocephalus townsendi*, from Princeton, San Mateo County, California. Abstract 62. Second Biennial Conference of Research in California's National Parks. Univ. Calif., Davis, 5-7 Sept. 1984.

STARKS, E. C.
1922. Records of the capture of fur seals on land in California. Calif. Fish Game 8:155-160.

STEWART, B. S.
1981. The Guadalupe fur seal (*Arctocephalus townsendi*) on San Nicolas Island, California. Bull. S. Calif. Acad. Sci. 80:134-136.
1985. Population biology of pinnipeds at San Miguel Island, 10 June through 29 August 1985. HMRI Tech. Rep. 85-185, Hubbs Mar. Res. Cent., San Diego, CA, 26 p.

STEWART, B. S., and P. K. YOCHEM.
1984. Seasonal abundance of pinnipeds at San Nicolas Island, California, 1980-1982. Bull. S. Calif. Acad. Sci. 83:121-132.

STEWART, B. S., P. K. YOCHEM, R. L. DeLONG, and G. A. ANTONELIS.
In press. Trends in abundance of pinnipeds on the Southern California Channel Islands. Proc. Third Calif. Channel Islands Symp., 2-6 March 1987, Santa Barbara, CA.

TOWNSEND, C. H.
1899. Notes on the fur seals of Guadalupe, the Galapagos, and Lobos islands. *In* Jordan, D. S. (ed.), The fur seals and fur-seal islands of the North Pacific Ocean, Part III, p. 265-274. U.S. Gov. Print. Off., Wash., D.C., 629 p.
1930. Guadalupe fur seal in 1929. Bull. N.Y. Zool. Soc. 33:32.

WALKER, P. L., and S. CRAIG.
1979. Archaeological evidence concerning the prehistoric occurrence of sea mammals at Point Bennett, San Miguel Island. Calif. Fish Game 65:50-54.

WEBBER, M. A.
In press. A northern record for the Guadalupe fur seal (*Arctocephalus townsendi*) from Monterey Bay, California. Bull. S. Calif. Acad. Sci.

Rearing of Twin Offspring to Weaning in Antarctic Fur Seals, *Arctocephalus gazella*

D. WILLIAM DOIDGE
Department of Renewable Resources
MacDonald College of McGill University
21111 Lakeshore Road, Ste-Anne-de-Bellevue
Quebec HX9 1CO, Canada

ABSTRACT

Growth rates of two sets of twin Antarctic fur seal pups, *Arctocephalus gazella*, (male-female, female-female) and feeding attendance patterns of their mothers were compared with those of single offspring.

The female-female twins had growth rates and weaning weights within the range of single female pups. The male of the female-male pair spent more time suckling and had a significantly higher growth rate than his sister. Growth in both pups was substantially reduced compared with single pups. Feeding-attendance patterns of both mothers was not significantly different from those rearing single offspring although the energy costs of pup rearing increased by 75%.

Measures of feeding or attendance duration should be used with caution as potential indicators of prey abundance or energy flow to offspring. Strategies for sexual selection and factors acting against increased litter size in fur seals are discussed.

INTRODUCTION

The incidence of twinning is very low in otariids; no published records of otariid twins surviving to weaning were known to Spotte (1982) and only one has been reported since for the subantarctic fur seal, *Arctocephalus tropicalis* (Bester and Kerley 1983). Presumably there is strong selection pressure for single offspring per litter, but it is not clear to what extent this acts during rearing (e.g., the inability of the mother to find or transfer enough food), when juvenile (e.g., during the first winter of independence), or when immature (e.g., in terms of recruitment to the breeding herd). A detailed study of the performance of females rearing two pups should illuminate the first of these and perhaps also provide useful information on the limits to performance of females during lactation.

During a 5-year study of attendance by females and pup growth in Antarctic fur seals, *A. gazella*, at South Georgia (lat. 54°S, long. 38°W), a birth of twins (male-female) was witnessed at Bird Island in 1978, but both pups died within a month of birth (R. D. Bell 1979). At Schlieper Bay on two occasions (1979 and 1981) females were seen consistently suckling the same two pups in circumstances almost certainly attributable to twin births. The simultaneous suckling of two pups, although infrequent, does occur at both high- and low-density breeding beaches, but under circumstances different from those recorded above and involving at least one pup which is not the offspring of that female.

This paper compares the pattern and duration of the feeding-attendance cycles of the two females rearing twins with those of females having single offspring in the same season (Doidge et al. 1984a; Doidge unpubl. manuscr.) in order to identify any differences in maternal performance. Similarly the growth of twin pups are compared with those of single offspring (Doidge et al. 1984b; Doidge unpubl. manuscr.) to assess the extent and consequences of possible selection against twin pups during the rearing period.

METHODS

The patterns of feeding trips to sea by the females and their attendance ashore while nursing pups were established by paint-marking the female and tagging the pups. The breeding beach and an area of roughly 20 ha surrounding it were checked twice daily at approximately 0500 and 1700 local time (GMT - 3 hours). These methods are described in greater detail in Doidge et al. (1986) and Doidge (unpubl. manuscr.).

On 19 December 1979 a female (designated CT) was seen suckling two pups. She and the two pups were given prominent identification marks using enamel paint. The pups were double tagged on the fore-flippers; the male (monel tag no. 59551, Allflex medium yellow 151) on 9 January and the female (monel 59602, Allflex 202), on 11 January 1980. The pups, which will be referred to by their Allflex tag numbers, were weighed at irregular intervals until 10 February when we left the study area. On a subsequent visit (3-6 March), the pups, although small, had completed molting and were in apparently healthy condition.

A second female (designated TM) was observed nursing two pups on 9 December 1981. The pups had wet and shiny fur indicating that they had been born only a few hours previously. These pups, which were both female, were weighed, double tagged (Allflex medium white 21-22, 23-24) and returned to their mother. Pup growth and the females' feeding-attendance cycles were monitored until weaning.

Table 1—Maternal feeding-attendance pattern of *A. gazella* cow CT.

	Observed cycle number								
	1	2	3	4	5	6	7	8	9
Cow at sea (d)	4	5	3	3	4	5	6	6	—
Cow ashore (d)	1	1	1	2	3	2	2	3	1

Table 2—Comparison of feeding-attendance data of *A. gazella* female CT (with male-female twins) and those females with single offspring, Schlieper Bay 1979-80, during the first six cycles[a].

	Female CT	Other females (n=8)[b]
Mean days at sea	4.0 ± 0.9 (6)	3.5 ± 1.9 (48)
Mean days ashore	1.7 ± 0.8 (6)	1.7 ± 1.0 (48)
Time at sea (%)	71 ± 11 (6)	65 ± 16 (48)

[a]Number of cycles used by Doidge et al. (1986).
[b]Doidge et al. (1986).

Table 3—Feeding-attendance pattern of *A. gazella* female TM from the end of the perinatal attendance period until weaning, Schlieper Bay, 1981-82.

	Observed cycle number															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Cow days at sea	2	2	3	4	4	3	4	5	4	5	7	4	5	7	5	6
Cow days ashore	3	2	1	2	2	3	1	3	2	2	2	3	2	2	4	10
Days not with pup 22	2	2	3	4	4	3	4	6	4	5	7	4	6	7	5	7
Days not with pup 24	2	2	—	8	4	3	4	5	4	6	7	4	5	8	8	—
Days with pup 22	3	2	1	2	2	3	1	2	2	2	2	3	1	2	3	4
Days with pup 24	3	2	—	2	2	3	1	3	2	1	2	3	2	1	1	—

Table 4—Comparison of feeding attendance data (birth to weaning) of *A. gazella* female TM with female twins and females with single pups, Schlieper Bay, 1981-82.

	Female TM	Other females[a]
Perinatal attendance (d)	6	7.2±0.9
Total days at sea	70	68±7
Total days not with pup 22	73	—
Total days not with pup 24	70	—
Total days ashore	38	40±9
Total days with pup 22	35	—
Total days with pup 24	28	—
Number of feeding trips	16	16±3
Time at sea (%)	65	62±5

[a]Doidge (unpubl. manuscr.).

Growth rates were determined by linearly regressing weight on age for known-age pups 22 and 24, and weight on calendar date for pups 151 and 202. (See Doidge et al. 1984b for further details of these methods.)

RESULTS

The data gathered on the two sets of twins were slightly different. Although cow TM and her female pups (22, 24) were followed from birth to weaning, cow CT and pups (male 151, female 202) had an unknown birthdate and were observed for only 9 feeding-attendance cycles during pup rearing which usually lasts about 16 cycles (Doidge et al. 1986). Therefore, the comparisons with mothers with single pups will be made separately for each set of mothers and twins.

Maternal feeding-attendance performance

The mean duration of feeding trips, shore attendance periods, and proportion of time spent at sea for female CT (Table 1) are not significantly different from those of females with single offspring at Schlieper Bay in 1979-80 (Table 2). Table 3 lists the complete feeding-attendance cycles from the end of the perinatal attendance period to weaning for female TM. The total numbers of days at sea and ashore, the number of feeding trips made, and the duration of the perinatal attendance period are statistically indistinguishable from those of females with single female offspring at Schlieper Bay in 1981-82 (Table 4).

Pup performance

Male-female pair—Male pup 151 grew at the rate of 61 g/d which was significantly greater ($F_{1,24}$ 2.53, P<0.05) than the 26 g/d of female pup 202 (Fig. 1). The growth rates of both CT's pups were substantially lower than those of single offspring, were outside the range of pup growth rates found in five seasons of pup weighings at South Georgia (Doidge et al. 1984b), and were lower than those of pups followed to weaning in 1981 (Doidge unpubl. manuscr.).

During 8.7 hours of observation of female CT during the first four attendance periods witnessed, the male pup spent significantly more time suckling than the female (147 vs. 105 minutes, χ^2=9.02, P<0.05). In both pups, growth rate decreased after tagging. This may be coincidental or caused by the disturbance associated with suckling observations or pup weighings. Payne (1979) believed that tagging was detrimental to young pups since 10% of those he tagged died. However, this is not unexpected because pup mortality ranges between 17 and 30% at the site where he was working (Doidge et al. 1984a). Also, Doidge (unpubl. manuscr.) showed that tags had no effect on pup growth rates.

Female-female twins—Although both pups were female, they spent slightly different amounts of time with their mother. Pup 24 failed to make contact with female TM on the third attendance period (Table 3), and did not suckle until 8 days later. The lighter pup (24) spent less time with the mother and weaned at an earlier age and date.

Growth rates and estimated weaning weights of pups 22 and 24 are listed in Table 5 (see also Fig. 2). The growth rate, weaning weight, and age at weaning of pup 22 are very similar to those of single female offspring followed to weaning in the same season (Doidge unpubl. manuscr.). Although pup 24's growth rate, weaning weight, age at weaning, and date of weaning are low, they are within the range of single female offspring (Doidge unpubl. manuscr.).

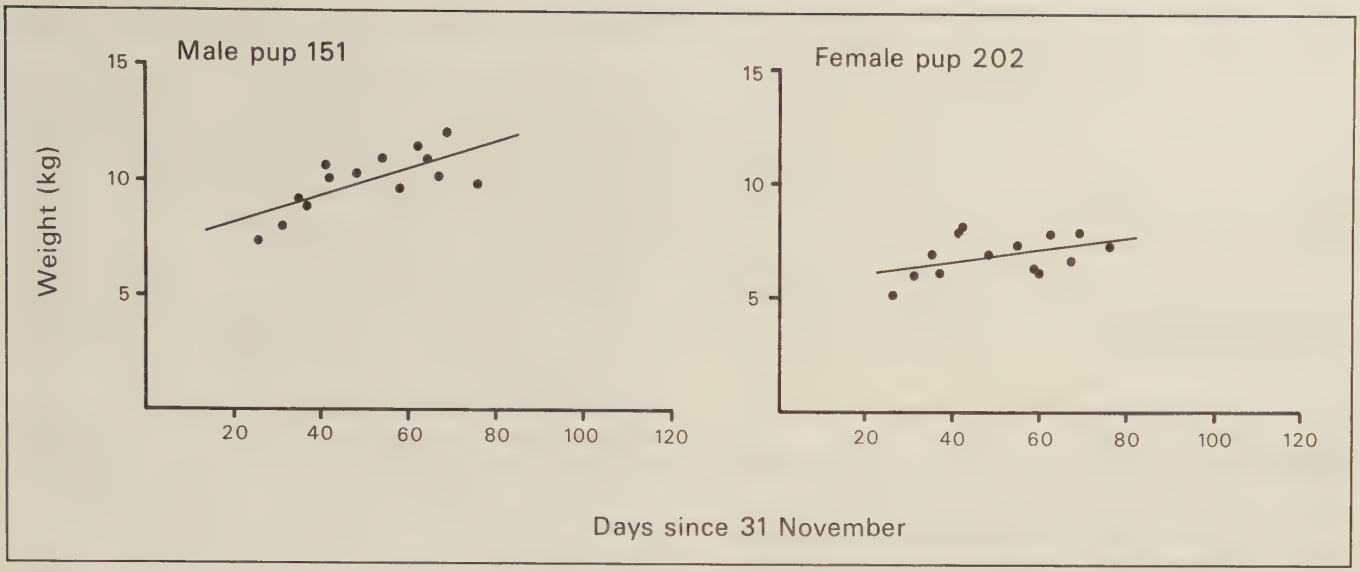


Figure 1—Growth of male and female twins, Schlieper Bay 1979-80.

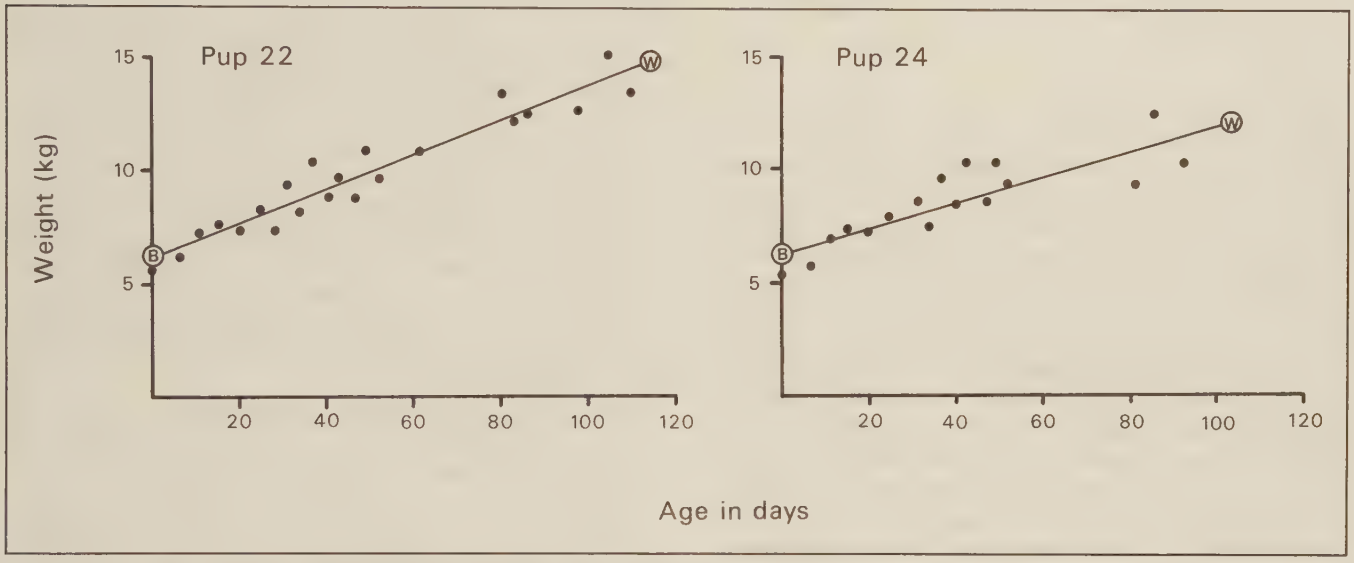


Figure 2—Growth of female twins and estimated birth (B) and weaning (W) weights, Schlieper Bay 1981-82.

Table 5—Comparison of growth parameters of twin female pups of *A. gazella* cow TM with those of single female pups, Schlieper Bay, 1981-82.

	Pups of female TM			Single female pups[a] $n=21$	
Growth parameters	22	24	Total	Mean	Range
Date of birth	9/12/81	9/12/81	—	9/12/81	21/11-24/12/81
Date of weaning	1/04/82	22/03/82	—	1/04/82	21/03-12/04/82
Weight at birth (kg)	5.8	5.3	11.1	—	—
Estimated weight at birth[b] (kg)	6.2	6.4	12.6	5.7	4.0-7.4
Estimated weight at weaning[b] (kg)	14.6	12.1	26.7	14.7	10.1-18.7
Growth rate[b] (g/d)	75	55	—	78	53-107
Age at weaning (d)	114	104	—	113	90-126

[a]Doidge (unpubl. manuscr.).
[b]Estimated from linear regression of weight on age.

Maternal energy cost

Preliminary estimates of the cost of pup rearing in Antarctic fur seals, partitioned into energy consumption required to fuel fetal growth, pup metabolism, and weight gain, have been made by Doidge et al. (1984b) based on metabolic rates of northern fur seals, *Callorhinus ursinus* (Blix et al. 1979), time activity budgets of *A. gazella* (Doidge unpubl. data), and the energy contents of tissues (Diem and Lentner 1970). Using the same technique, the energy required to raise twin female offspring for female TM (Table 6) was 3215 MJ or 1.74 times the energy needed for rearing the average single female pup.

Table 6—Comparison of maternal energy requirements (MJ) of *A. gazella* female TM (with female twins) and females rearing single offspring.

	Pups of female TM			Females with single pups[a]
	22	24	Total	
Pup mass at birth	61	63	124	61
Mass gain birth to weaning	230	173	403	255
Pup metabolism	1,479	1,209	2,688	1,532
Total	1,770	1,445	3,215	1,848

[a]Doidge (unpubl. manuscr.).

DISCUSSION

The successful rearing of twin pups to weaning, without a concomitant change in feeding or attendance duration, reinforces the conclusions of Doidge et al. (1984b) that these data should be used with caution as potential indicators of prey abundance or energy flow to offspring. The incidence of twinning is low in otariids, so it is interesting to view its consequences for both mother and pup when it does occur.

Consequences for mother

Although there was no difference in time spent at sea between mothers of single and twin pups, it is possible the latter were working harder (per unit time) to secure more prey to meet increased energy demands. This is a consideration, since females spend only 20% of their time at sea actually diving in search of prey (Kooyman et al. 1986). Although the time spent ashore is the same as that of mothers of single pups, the amount of energy transferred to the pup is increased 1.74 times. Why then do mothers of single pups not increase the energy transferred to their pups? It appears that under the conditions existing at South Georgia in 1981, the limiting factor for pup growth involves milk transfer rather than cow foraging performance. Doidge (unpubl. manuscr.) found that weaning weight increased with the total number of days spent ashore by the mother during the lactation period, but that no significant relationship existed with the number of maternal days at sea. The time spent nursing and the amount of energy transferred during a shore attendance bout is more dependent on the pup's, rather than the mother's, nursing ability since suckling is a relatively passive activity for the female. (If milk is available she need only expose her teats.) Also, the unusual method of weaning in this species, where the pup leaves the mother rather than vice versa (Doidge et al. 1986) supports the hypothesis that the pup tends to govern milk intake.

High growth rates and the rapid rate of increase of the population indicate that food availability during the breeding season has not generally been a limiting factor for fur seals at South Georgia (Doidge et al. 1984b). Thus, it appears that under the conditions found in 1979-80 and 1981-82, females with single pups were capable of supplying more than enough milk to meet pup demands and that pup growth was limited by the pup's own suckling behavior. However, since neither female rearing two pups was able to wean both pups at average weaning weights, apparently conditions were not good enough to allow the rearing of two normal pups.

Consequences for the offspring

Of the four pups, only pup 22 (of the female-female pair) had an average growth rate, length of lactation period, and weaning weight when compared with single pups. Her sister, pup 24, showed a 30% reduction in growth rate, an 18% drop in weight at weaning, and a lactation period shorter by 8%. Thus, one female pup was average and the other slightly lighter, although not outside the range expected for single female pups. Presumably, the chances of pup 22 surviving to breeding were equal to that of the average female pup surviving to weaning that season, and pup 24's chances were slightly less but still better than some single female pups (assuming that survival and weight are directly related).

In the male-female pair, the growth rate of both pups was reduced; the male being 23% lower and the female 51% lower than the average single pup. Although the male was superior to the female pup in terms of competition for access to the mother for milk (see "Pup performance; Male-female pair"), the males still have a lower than average growth rate.

Factors acting against twinning

If the combined probabilities of the twins rearing offspring to breeding were greater than that for single offspring, twinning would be favored regardless of the sex of the original twins. However, if an adult female bears a male and a female pup (50% of the expected frequency of dizygotic twins), then the chances of both offspring surviving to breeding would be reduced. The male pup, even if it survived its first winter of independence, would be unlikely to attain a body size capable of competing for territories with other males; the female pup's chances of surviving to breeding are also reduced since her brother has taken resources (milk) which might have been invested more profitably in her.

Male-male twins would be a still more extreme case where neither would likely become sufficiently large to compete against single male offspring for territories.

In the case of female-female pairs, the chances of survival to breeding are slightly greater than male-male or male-female pairs since pup energy requirements are closer to being met.

Thus, in only 25% (female-female twins) of the possible outcomes of dizygotic twins can maternal breeding success be greater than that of single mothers, and even in this case reproductive output would, at best, only be doubled. In the monozygotic case, where the sex of the offspring could equally be male or female, the average breeding success of mothers of twins would still not exceed that of single mothers for the reasons just mentioned. Presumably, under the conditions in which the otariids evolved, the cost to lifetime reproductive success of increasing litter size has outweighed the benefits. So, although conditions are generally very favorable for *A. gazella* at the present time, there is no evidence that the incidence of twins is any greater than other less well-studied otariids.

ACKNOWLEDGMENTS

I conducted this study under the employ of the British Antarctic Survey. I thank A. P. Martin and R. D. Bell for assistance in the field and RRS *John Biscoe* and the Royal Navy for logistic support. J. P. Croxall constructively criticized the manuscript.

CITATIONS

BELL, R. D.
1979. Progress of fur seal pup mortality programme, ZV15 Bird Island 1978/79. Unpubl. manuscr., Br. Antarct. Surv., Madingley Road, Cambridge CB3 OET, U.K.

BESTER, M. N., and G. I. H. KERLEY.
1983. Rearing of twin pups to weaning by subantarctic fur seal *Arctocephalus tropicalis* female. S. Afr. J. Wildl. Res. 13:86-87.

BLIX, A. S., L. K. MILLER, M. C. KEYES, H. J. GRAV, and R. ELSNER.
1979. New born Northern fur seals (*Callorhinus ursinus*) - Do they suffer from the cold? Am. J. Physiol. 236:R322-R327.

DIEM, K., and C. LENTNER (editors).
1970. Documenta Geigy scientific tables. Geigy Pharmaceuticals, Macclesfield, U.K., 809 p.

DOIDGE, D. W., J. P. CROXALL, and J. R. BAKER.
1984a. Density-dependent pup mortality in the Antarctic fur seal *Arctocephalus gazella* at South Georgia. J. Zool. (Lond.) 202:449-460.

DOIDGE, D. W., J. P. CROXALL, and C. RICKETTS.
1984b. Growth rates of Antarctic fur seal *Arctocephalus gazella* pups at South Georgia. J. Zool. (Lond.) 203:87-93.

DOIDGE, D. W., T. S. McCANN, and J. P. CROXALL.
1986. Attendance behavior of Antarctic fur seals. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur seals: Maternal strategies on land and at sea, p. 102-114. Princeton Univ. Press, Princeton, N.J.

KOOYMAN, G. L., R. W. DAVIS, and J. P. CROXALL.
1986. Diving behavior of the Antarctic fur seals. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur Seals: Maternal strategies on land and at sea, p. 115-125. Princeton Univ. Press, Princeton, N.J.

PAYNE, M. R.
1979. Growth in the Antarctic fur seal *Arctocephalus gazella*. J. Zool. (Lond.) 187:1-20.

SPOTTE, S.
1982. The incidence of twins in pinnipeds. Can. J. Zool. 60:2226-2233.

Age-Specific Reproductive Behavior in Northern Fur Seals on the Commander Islands

VALERY A. VLADIMIROV
VNIRO
17 F. Krasnoselskaya
Moscow B-140
U.S.S.R.

ABSTRACT

Prolonged observation of large numbers of known-age tagged northern fur seals on Urilie rookery, Commander Islands, has given new insights into reproductive processes of males and females that must be incorporated into existing population models and forecast procedures. A synopsis of the important results is: 1) the number of pups born varies directly with the summed number of young (5-7 years) and old (>15) females, and with territorial males aged 8 years; 2) of 130 known females observed over 4-7 years, 57% gave birth sequentially with no break in pregnancies; 3) the pregnancy rates differ by year and age class and are subject to yearly fluctuations; 4) young females breed mostly from August to mid-September and greatly affect the age structure and number of pups born the following year; 5) most breeding is done by males aged 8 and 9 years; 6) the maximum number of bulls determined by visual counts does not exceed 50% of the total number in the population; 7) male territorial tenure varies by age such that a complete replacement of males occurs twice during the main breeding season; 8) about 30% of bulls age 8 and older never try to establish a breeding territory but reside on bachelor grounds.

INTRODUCTION

In recent years scientists have developed mathematical models of fur seal population dynamics, methods of theoretical assessment, and forecasts of biological characteristics such as the number of pups born, optimal commercial exploitation, age-sex structure of reproductive groupings, and so on (Andreev et al. 1978; Bulgakova 1972, 1973; Borodin and Vladimirov 1975; Chapman 1964, 1973; Chelnokov 1977; Eberhardt 1981; Ichihara 1971; Johnson 1968; Kolesnic and Kogay 1977; Kuzin and Panina 1977; Lander 1975, 1979, 1981; Nagasaki 1961; Nesterov 1978; Skaletskaya et al. 1980; Smith and Polacheck 1981; Timofeeva et al. 1977; York and Hartley 1981).

In 1978-82 our investigations on Urilie rookery of Medney Island (Commander Islands) showed that many of the most important biological parameters which are basic to quantitative models and estimation methods are imprecise to a great extent. Some significant characteristics of the reproductive process were not taken into account at all because they remained unknown until now. These omissions must inevitably result in more or less misrepresentation and non-representativeness of the theoretical results obtained. It is very difficult to forecast population dynamics, conduct mathematical modeling of the populations, and simultaneously solve the problems connected with monitoring without a detailed knowledge of all aspects of fur seal reproductive biology.

Urilie rookery, where no sealing has been conducted for more than 50 years, is practically under natural conditions. Due to this fact specific details of age-sex structure, social behavior, and organization of reproducing animals are closer than any other fur seal rookery to "wild" conditions, and can thus be considered to be close to optimum for reproduction and population growth. This statement is confirmed by the fact that Urilie rookery is the only one on the Commander Islands where fur seal numbers have been steadily increasing over the past 10 years.

Data characterizing the reproductive biology of female fur seals are numerous (Bartholomew and Hoel 1953; Bigg 1979; Bychkov 1964, 1969; Craig 1964; York 1979a,b, 1983; Yoshida 1982). However, there are no data on the continuity or periodicity in reproduction of individual females of different ages over long periods.

A significant factor in reproductive efficiency is the number of breeding males. This factor becomes especially important when males are reduced by harvesting to a level which might jeopardize insemination of all mature females. Such a situation apparently took place on the Commander Islands early in the 1970's. When bull numbers are high, annual fluctuations do not directly influence reproductive efficiency. Finally, the age composition of fur seal males taking part in reproduction has a great influence on the regenerative process in fur seals. In 1977-81 we obtained data characterizing the seasonal dynamics by age of the bull-producers.

METHODS

This work is based on data collected on Urilie rookery in 1977-82. Investigations were based mainly on regular visual observations of tagged known-age animals. Observations were conducted both on the entire rookery and on a specially established experimental area 40×20 m. On the special study area in 1978-81 regular observations were performed from a watch tower two or three times per day (for a total of 6 hours per day) every day if weather was favorable. Tag numbers were read with the aid of a telescope (30,

40, and 60 power). Some data were also collected by V. N. Sadovov (VNIRO) in 1977.

Observations extended from the end of May to the end of October in the various years of this study (Table 1). We observed the reproductive cycles of 130 individually identified females that were recorded annually for at least 4 (maximum of 7) years running. This study was possible because of the strong homing instinct of northern fur seals; almost all females arrived annually to the same places on the rookery where they were previously seen.

Several criteria were used to determine whether a given female produced a pup in a given year. Females were classified as parous if their pups were observed with them, or if they showed search behavior for a pup, or had unmistakable symptoms of lactation such as swollen teats. It was much more difficult to assign females to the nonparous category. Data analysis for 1978-79 and 1981 (Table 2) showed that to obtain good direct or indirect evidence of pup presence most females (mean 97.6%, range 96.0-98.1%) had to be observed five times. Based on these data, we concluded that females whould be considered nonparous if in five or more observations either no pup was observed or the female showed neither behavioral nor physiological signs of pup presence. Females for which fewer than five observations were made were assigned to the undetermined reproductive category. However, such females were likely nonparous for that year because infrequent and irregular presence on a rookery is diagnostic behavior for females that have no pup. These concerns do not apply to the 1977 data which were collected by V. N. Sadovov using different field methods. None of the females was observed in 1977 more than four times, and most of them were seen only once. Therefore the 1977 data gave no basis for assuming that females without pups had missed pregnancy, so all females not seen with pups were assigned to the undetermined category.

To analyze for seasonal changes in fur seal age structure we used a coefficient of tagging that was specific to each year class and rookery of origin, and a coefficient of tag loss that was specific to each age class and population. The coefficients of tagging (untagged/tagged ratio) and of tag loss (number losing tags/number retaining tags) were based on data in the NPFSC Joint Reports and in Andreev et al. (1978); see Vladimirov (1978) for methods. Tag loss for females aged 2-5 years was assumed to be equal to that of bachelors of the same age and origin. Tag loss for all older females, and for all bulls irrespective of age or origin, was assumed to equal 0.55, the maximum rate for 5-year-old bachelors.

RESULTS

In total, 7,027 tagged fur seals of different age and sex were observed. These included 2,759 males (461 bulls) and 4,268 females.

Females

The number and age composition of reproducing females are of great importance to forecasting fur seal population dynamics because they are closely tied to annual pup production (Vladimirov 1982). Table 3 shows the average age composition (average proportion of onshore females in each age group) of tagged females at the June-July peak of the reproductive seasons from 1977 to 1982. The table also shows for each age group the proportion of the summer-autumn count for each age group that this June-July number represented. Clearly, the majority of the female population at almost any time of year comprises animals 6-15 years of age. Furthermore, the difference in age composition between the summer and autumn populations lay basically in the later time of arrival at the rookeries of many females 3-5 years of age and younger.

The age composition shown in Table 3 is an average of 6 years of observations. Actually, the age composition was not stable, but fluctuated from year to year, especially in the youngest age groups. Table 4 shows these yearly variations for each age group of the youngest females, and for combined age groups for all others.

Table 3 also shows that the pregnancy rates among females varied by age class. Among 702 tagged females with determined reproductive status that appeared on the rookery in June-July, the average pregnancy rate for all age classes combined was 82.6% (range 77.7-85.9% in various years). Females aged 4-5 and >15 years had the lowest average pregnancy rates. Presently females at Urilie rookery begin to give birth at age 4 years. But the total percentage of 4-5 and even 6-year-olds that are pregnant can be precisely determined only from animals that are collected pelagically because not all of these females (especially 4-year-olds) land on the islands.

Data obtained from seals collected pelagically in the Commander Islands area in autumn 1978 show that not more than 30-35% of 4-year-olds and not more than 65-70% of 5-year-olds are pregnant (Vladimirov et al. 1979; North Pacific Fur Seal Commission 1981).

Visual observations on shore give estimates of pregnancy rates for females aged 7 and older that are almost equal to estimates from pelagic collections. For instance, from 1978 to 81 the estimated

Table 1—Dates of observation periods on Urilie rookery, 1977-82.

Year	Period
1977	June 16-July 31
1978	May 26-July 30
1979	June 21-Sept 27
1980	June 25-Aug. 23
1981	May 22-Oct. 28
1982	June 13-Aug. 19

Table 2—Number of observations necessary to visually link pups with postpartum females on Urilie rookery, in 1978-79 and 1981.

		Number of observations[1]										
		1		2		3		4-5		>5		
Year	N^2	n^3	%	n	%	n	%	n	%	n	%	$\bar{x}^4$
1978	123	52	42.3	35	28.5	20	16.3	11	8.8	5	4.1	2.1
1979	137	57	41.3	42	30.7	21	15.3	12	8.7	5	3.6	2.3
1981	531	255	48.0	163	30.7	64	12.1	39	7.3	10	1.9	1.9
Total	791	364	46.0	240	30.3	105	13.3	62	7.8	20	2.5	2.0

[1]Number of encounters in which a pup was directly or indirectly linked with a female.
[2]The total number of females identified by year.
[3]The number of fur seal females identified as having a pup.
[4]The average number of observations necessary to find a pup or to identify its presence.

Table 3—Age composition, summer/autumn arrival, and pregnancy rate by age for fur seal females at Urilie rookery during the breeding seasons of 1977-82.

Age (yr)	N %	N_1 %	N_2 %	P_r %	Age (yr)	N %	N_1 %	N_2 %	P_r %
1	—	2.1	—	—	12	7.3	0.9	95.7	88.4
2	—	5.7	—	—	13	5.8	4.7	99.2	72.9
3	0.4	8.2	0.8	—	14	5.9	5.5	100.0	81.1
4	3.6	7.9	36.6	72.3	15	5.6	3.2	98.7	81.1
5	7.8	10.3	74.2	77.8	16	3.9	2.6	100.0	80.8
6	9.8	10.2	87.3	80.2	17	2.8	2.4	100.0	74.2
7	10.3	5.6	96.7	86.2	18	1.3	0.3	100.0	78.9
8	7.9	6.6	98.5	87.3	19	0.6	1.0	100.0	50.0
9	8.5	5.5	90.8	93.3	20	0.4	0.3	100.0	50.0
10	8.7	8.3	97.7	90.5	21	0.1	<0.1	100.0	33.3
11	9.3	8.7	97.8	82.7	22	0.1	<0.1	100.0	[1]100.0

N Age composition of fur seals on land in June-July as a percent of the average summer number observed 1977-82.

N_1 The October age composition of females onshore as a percent of their number in that month.

N_2 The June-July number of females onshore in each age class as a percent of females in that age class observed in summer-autumn of the same years.

P_r The percent of postpartum females in each age class in June-July.

[1] $N=1$; therefore no conclusion about pregnancy rate should be drawn.

Table 4—Yearly fluctuations in the age structure of female fur seals at resident Urilie Rookery in June-July, 1977-81, based on reading tags of known-age animals.

Age group (yr)	Percentage of females by years[1]				
	1977	1978	1979	1980	1981
3	—	—	0.4	0.1	0.3
4	2.2	0.9	5.6	6.9	4.0
5	9.0	7.8	3.7	9.7	8.9
6	14.0	11.2	9.7	5.8	12.1
7	12.2	7.7	14.8	9.2	5.0
3-7 (junior)	37.4	27.6	34.2	31.7	30.3
8-15 (middle-aged)	57.8	66.4	56.4	60.5	57.0
>15 (elder)	4.8	6.0	9.6	7.8	12.7

[1]Percentages were estimated from the calculated number of females (taking into account the rates of tagging and tag loss).

pregnancy rate from observations at Urilie Rookery was 83.7% compared with 84.2% from the pelagic collection (Vladimirov et al. 1982). However, average pregnancy rate for females 4-6 years cannot be estimated from observation because not all of these females come ashore on the rookery. Therefore, shore observations can be used to substitute for pelagic collections to estimate pregnancy rates for most females.

The number and pregnancy rate of young females coming to the rookery have a great effect on the total age structure of the breeding group, and on the number of pups born. Figure 1 shows that changes in the number of pups born correspond closely to the total percentage of females aged 5-7 years, and less closely to females aged >15 years. The correlation coefficient for the comparison of pups born with females 5-7 years plus females >15 years was 0.94. No correspondence was found between the number of middle-aged females and pups born. Old females produce only about 8.8% of the total number of pups born (average of 4 years data) while young females (5-7 years) produce about 22.1%. Therefore, the number of older females effects the number of pups born to a lesser extent than does the number of young females. The number of young females depends on the initial number in different year classes, the rate of natural mortality (which is highest and most variable in young animals), as well as time of maturation and other factors. The number of middle-aged females apparently does not undergo such sharp fluctuations which explains why their numbers do not correlate with pup numbers. Figure 1 also shows a correlation between variations in the proportion of the total bull stock (ages 8 years and older) that are of age 8 years, and the birth of pups the next year. However, no such correlation was found in recent years when the number of bulls became very high.

Table 3 also shows that young females, aged 3-5 or 6 years, tended to arrive later in the season than older females. An analysis of data from 469 postpartum tagged females showed that the mass arrival of pregnant females begins in the last five days of June. By July 25 the overwhelming majority (average 92.1%, range 91.0-93.2%) of the pregnant females have already arrived. By 31 July, 97.4% (range 96.5-98.1%) have arrived. Effectively, the monthly period

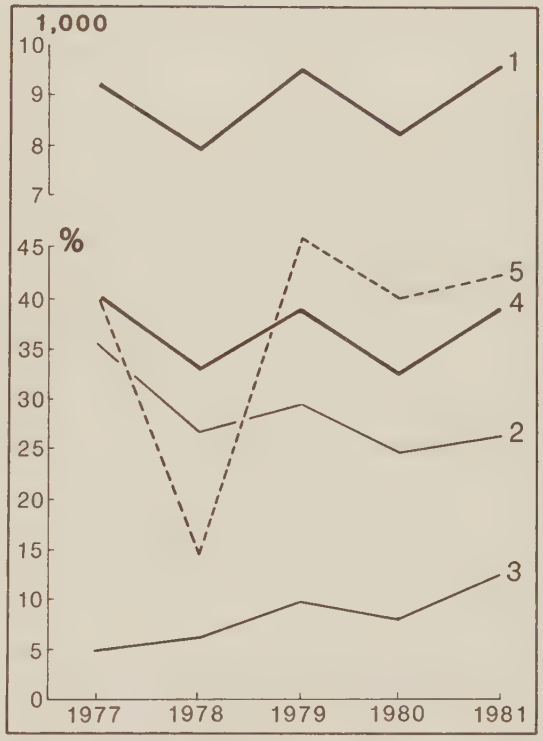


Figure 1. Population dynamics of (1) fur seal pups born on Urilie rookery in 1977-81 compared with: (2) percent of female population aged 5-7 yr and (3) aged 15+ yr; (4) summed percent of these two groups; and (5) percent of previous year's bull population aged 8 yr.

from 25 June to 25 July can be considered the main reproductive period.

Additional data on the arrival dates of 514 females of different ages in 1979 and especially in 1981 (when observations ended in late October) showed the arrivals by July 31 of the following proportions of each age class that would eventually arrive: 3-year-olds, 0.8%; 4-year-olds, 36.6%; 5-year-olds, 74.2%; 6-year-olds, 87.3%; 7-10 year-olds, 95.9%; 10+ year-olds, 99.2% (Table 3). Thus, females at age 6 years and older first appeared on the rookery almost entirely during June-July. The younger their age, the later females arrived. The proportion of females aged 3-5 years that

Table 5—Periodicity of reproduction in fur seal females on Urilie rookery, 1978-83.

Female no.	Year class	Origin	Age (yr) 2	3	4	5	6	7	8
1	1977	U	–	–	+	+	–		
2	〃	〃	–	–	+	+	+		
3	〃	〃		–	+	+	+		
4	〃	〃		–	–	–	+		
5	〃	〃		–	–	+	+		
6	〃	〃		–	+	+	+		
7	〃	〃		–	+	+	–		
8	1976	〃		–	+	+	+		
9	〃	〃		–	+	+	+	+	
10	〃	〃		–	+	+	?	+	
11	〃	〃		–	–	+	+	+	
12	〃	〃		–	?	+	+	+	
13	〃	〃		–	?	+	+	+	
14	〃	〃		–	?	–	?	+	
15	〃	〃		–	–	+	+	+	
16	〃	〃		–	+	–	+	+	
17	〃	〃		–	+	+	?	+	
18	〃	〃		–	–	+	+	+	
19	1975	〃			?	?	+	+	
20	〃	〃			?	?	+	+	
21	〃	〃			?	?	+	+	
22	〃	〃			?	?	?	?	
23	〃	〃			?	?	+	?	
24	〃	〃			?	?	?	+	
25	〃	〃			?	?	+	?	
26	〃	〃			?	?	?	?	
27	〃	〃			?	?	+	+	
28	〃	〃			+	?	+	+	+
29	〃	〃			?	?	?	?	?
30	〃	〃			?	?	?	+	?

Female no.	Year class	Origin	Age (yr) 4	5	6	7	8	9	10	11	12	13
31	1975	U	?	?	–	?	+					
32	〃	〃	?	?	+	?	+					
33	〃	〃	?	–	+		+					
34	〃	〃	?	?	+	?	+					
35	〃	〃	?	?	+	+	+					
36	〃	〃	?	–	–	–	+					
37	〃	〃	?	?	?	?	?					
38	1974	〃		+	+	+	+					
39	〃	SE		+	+	+	+	–				
40	1973	U	+	+	–	–	+	+	+			
41	〃	〃	?	–	+	+	+	+	+			
42	〃	〃	?	+	+	+	+	?	+			
43	〃	〃		+	+	+	+	+	+			
44	〃	〃		?	+		+	+	+			
45	〃	〃		+	?	+	+	+	+			
46	〃	〃			+	+	+	+	?			
47	1972	〃		?	–	+	+	+	+	+		
48	〃	〃		?	+	+	+	+	+	+		
49	〃	〃			+	+	+	+	+	+		
50	〃	〃			+	+	+	+	+	+		
51	〃	〃			?	+	+	+	+	+		
52	〃	SE			+	?	+	+	+	+		
53	〃	〃			+	+	+	+	+	+		
54	1971	↓			–	–	+	+	+	+	+	
55	〃	〃				+	+	+	+	?	+	
56	〃	U				?	+	+	+	+	+	
57	〃	〃				+	+	+	+	–	+	
58	〃	〃				+	+	+	+	–	+	
59	〃	〃				+	+	+	+	?	+	
60	1970	SE				+	+	+	+	+	+	+

Female no.	Year class	Origin	Age (yr) 7	8	9	10	11	12	13	14	15	16	17
61	1970	N	?	+	+	+	+		+				
62	〃	NW	?	?	?	+	+	+	+				
63	〃	SE	+	+	+	+	+	?	+				
64	〃	〃	?	+	+	+	?						
65	〃	〃	?	+	+	+	+	+	+				
66	〃	〃	?	?	+	+	+	+	+				
67	〃	U	?	+	–	+	+	+	+				
68	〃	〃	?	+	+	+	–	+	?				
69	〃	SE		+	+	+	+	+	+				
70	〃	〃		?	+	+	+	?	+				
71	〃	SE		+	+	+	+	+	+				
72	〃	〃		+	?	+	+	+	+				
73	〃	〃		?	?	+	+	+	+				
74	〃	〃		?	?	+	+	?	+				
75	1968	〃			+	+	+	+	+	?			
76	〃	〃			?	+	?	+	+	?	+		
77	〃	〃			?	?	?	+	+	+	+		
78	〃	P.Is.			?	+	+	+	+	+	+		
79	〃	SE				?	+	+	+				
80	〃	NW				?	+	?	+	?	?		
81	〃	U				?	+	+	+	+	+		
82	1967	N				?	+	+	?	+	+	+	
83	〃	〃				+	?	+	+	+	+	+	
84	〃	NW				+	+	+	+	+	+	–	
85	〃	U				?	?	+	+	+	+	?	
86	〃	SE					–	+	–	+	+	+	
87	〃	〃					+	?	+	–	+		
88	〃	〃					+	+	+	+	+	+	
89	〃	〃							?	+	+	+	
90	〃	SE					+		?	+	+	+	
91	1966	SE					?	+	–	+	+	+	+
92	〃	〃						?	+	+	+	+	
93	〃	N						?	+	+	+	–[x]	
94	〃	〃						+	+	+	+	=	+
95	〃	SE							?	+	?	–	

Female no.	Year class	Origin	Age (yr) 12	13	14	15	16	17	18	19	20	21	22
96	1966	SE		?	+	+	+	+					
97	〃	〃	?	?	+	+	?						
98	1965	〃	?	+	?	+	+						
99	〃	〃	?	?	?	?	+						
100	〃	〃	?	+	?	?	?						
101	〃	〃	?	+	?	?	?	+	–				
102	〃	〃		?	+	+	?						
103	〃	〃		+	+	+	+						
104	〃	〃		+	+	+	+						
105	〃	〃		?	–	–	+						
106	〃	〃		?	+	+	+	?	+				
107	〃	〃		+	+	+	?		+				
108	〃	〃		?	+	+	?	?					
109	〃	U		?	?	?	+						
110	〃	〃		?	?	+	+	–	+				
111	〃	〃			+	?	+		+				
112	1964	SE		?	+	?	–	+	+				
113	〃	〃		?	+		?	+	+	+			
114	〃	〃		?	+	+	+	+	+	+			
115	〃	〃			+	+	+	+	?				
116	〃	〃			+	+	+	+	+				
117	〃	〃			+	+	+	+	+				
118	〃	〃			+	?	–	+		?			
119	〃	〃			?	+	+	+	?				
120	〃	U		?	+	+	+	?	?	?			

Table 5—Continued.

Female no.	Year class	Origin	Age (yr) 12	13	14	15	16	17	18	19	20	21	22
121	"	N		?	?	?	–	–	?	?			
122	1963	SE			?	?	+		?				
123	"	"				?	?	?	+	?			
124	1962	"						+	+	+	?	?	
125	"	P. Is.				?	–	?	?	+	?		
126	"	"						?	?	?	?		
127	1961	SE					?	?	+	?	?	+	
128	"	P. Is.						+	+	–	–	?	
129	"	SE					?		?	?	–	–	?
130	"	"							?		+	?	

Note: + = A fur seal pup is available.
– = A fur seal pup is absent.
? = It is not precisely determined whether or not a pup was available.
P. Is. = Pribilof Islands; N = Northern rookery; NW = Northwestern rookery; SE = Southeastern rookery; U = Urilie rookery.
[x]The fur seal female came to the rookery with the scraps of a fishing net on her neck.

Table 6—Age composition and contribution to reproduction of reproductively active bulls on Urilie rookery, from 21 June to 31 July 1978-82.

Factors	Age of bulls (yr) 7	8	9	10	11	12	13	14	15
Kc (%)	14.9	21.1	24.2	17.2	13.2	4.8	2.6	0.8	0.7
Pc (%)	15.4	43.5	64.7	68.7	75.0	100.0	100.0	100.0	100.0
Tc (days)	5.5	12.9	18.8	16.9			12.0		
Cp (%)	2.0	17.4	37.4	21.5	14.2	4.4	2.5	0.5	0.1
Cp-1	3.0	20.3	36.0	31.3	29.1	27.1	22.9	21.6	10.8

Kc = Age group of bulls as a percent of the calculated number of bulls on a harem rookery is determined from the number tagged, corrected for rates of tagging and tag loss.
Pc = Proportion of bulls of every age group appearing on a harem rookery during the main reproductive period.
Tc = Mean duration of bull tenure on rookery.
Cp = Mean percent of females covered by bulls in each age group.
Cp-1 = Mean calculated number of females covered by one bull of the given age. The calculated number of females is based on the count of newborn pups corrected for the percent of non-pregnant females on the rookery in June-July.

appeared on the rookery in June-July seemed even lower than these numbers indicate because arrival at the rookery of numerous tagged females of these age classes which had not been observed in previous years, as well as the increase in presence of female year classes from year to year (Table 4), suggested that some of these animals did not appear on land at all. This was especially true for the younger females. The majority of nonpregnant females aged 4-6 years, both adult and immature, as well as females aged 2-3 years come to the rookery in late summer-autumn after the main reproductive season has ended (5-6 year-olds arrive in August, and 2-4 year-olds from August to October.

Most females have annual cycles of reproduction. The reproductive records of the 130 known females observed for at least 4 consecutive years show that after producing a pup once, most females (57%) usually continued to bear pups every year thereafter (Table 5). The annual cycle of pupping is most evident in females aged 6-15 years. Beyond 15 years, the number of years showing missed pregnancies increases, as indicated by the increasing assignment to the undetermined reproductive category in Table 5.

Table 5 also shows that the reproductive potential of female fur seals of different year classes can apparently differ greatly. We judge this from the frequency of missed pregnancies throughout the years each female was observed. In particular, Table 5 shows that 76.7% of females born in 1961-63, and 48.5% of females born in 1965 missed pregnancies. These results were confirmed by the 1978 pelagic sample of fur seals taken near Urilie rookery (Vladimirov et al. 1979) which showed that the 1961-63 year classes had a low percentage of postpartum females, but that pregnancy rate for the 1965 year class did not differ from the mean. The 1975 year class also appears to have an abnormally low pregnancy rate (Table 5), although this is now difficult to explain.

The average number of females aged 4-6 years that give birth in June-July (and the pregnancy rates for these age classes from pelagic sampling) is much higher than the average number of females one year younger that land during the previous June-July. For example, few 3-year-old females come ashore, but 30-35% of 4-year-olds are pregnant. This difference suggests that many young females copulate in August or early September. Our failure to see young females copulate on land suggests that they breed in the sea near shore. According to the calculations, up to about 30% of 3-year-olds, 20% of 4-year-olds, and 10% of 5-year-olds copulate in this period. Since these animals copulate as late as the first half of September, yet arrive in the second or third 10-day period of the following July, it appears that the gestation period (from fertilization to birth) is shorter for young females than for mature females (which is about 360 days).

Males

We define male producers as harem males (having females) and those occupying territories on the rookery, that is, males that are physically and physiologically capable of reproducing irrespective of the presence or absence of females at the moment of observation. We do not consider any males to be potential producers if they are unable to occupy their own territory during the breeding season.

Research conducted by the author and by N. N. Lyskin (Kamchatka Branch of TNIRO) showed that estimates of the maximum number of bulls (age 7 and older) obtained by visual head counts are far lower than those obtained from studying the seasonal arrival dynamics of tagged individuals. The study of tag returns showed that the maximum number of bulls which were simultaneously ashore, which usually occurred at the end of June, never exceeded 48.8% of total bull numbers in the population. Ichihara (1971) had similar results.

The rate of bull arrivals at the rookery in 1981 was analyzed by age and showed that of 142 tagged fur seal males aged 7-14 years, 11.3% had appeared on shore by late May, 74.4% by late June, 93.0% by late July, 99.3% by late August, and 100% by late September. No new bulls arrived in October. Thus the bulls' arrival was most intense in June; the majority of bulls appeared on the rookery throughout this period (63.1%). Some portion of bulls which participated in breeding in June-July returned again to the breeding areas at the beginning of autumn.

An analysis of the reproductive ability of bulls showed that males begin reproduction in fact only at age 8 in this relatively undisturbed population (Table 6). Formerly, 7-year-olds were included in the estimates of the reproductive male herd. However, our results show

that on average only 15% of young bulls at age 7 participate in reproduction. Because of seasonal peculiarities in the dynamics of the male age structure, distribution of males on the rookery, variations in the intensity of female arrivals, and other factors, 7-year-olds can cover not more than 2% of females during the main reproductive season. Therefore, the main breeding group is composed mostly of males 8 years old and older. The maximum duration of the bull's life is 15 years, according to 5 years of observation.

The estimate of reproductive contribution by bull age groups (Table 6) shows that the June-July average is about 25 females per bull producer in the main reproductive group. In reality this ratio is somewhat lower because the number of mature males calculated from tag returns is apparently lower than the actual number. This is because we lack data on immigrants of Pribilof Islands origin, where mass tagging ceased in 1969, and on bulls that lost tags (we used tag loss figures for 5-year-old males which are apparently lower than for adult males). Therefore, the real reproductive contribution per reproductively active, mature bull aged 8 and older is apparently about 20 females on Urilie rookery. This ratio seems to be optimum for reproduction. This value differs from the ratios given theoretically by other Soviet specialists (from 1:9-12 to 1:35-40).

Throughout the whole breeding season a constant, progressive rejuvenation of the age composition occurs among the bull producers. For example, according to the 1977-81 data, at the beginning of the breeding season (second 10-day period of June) bulls have the following age composition: 17.7% 8-year-olds; 22.2% 9-year-olds; 27.8% 10-year-olds; and 32.3% 10+ years of age. At the end of the harem season (third 10-day period of July) the age composition of bulls is: 19.0% 7-year-olds; 29.8% 8-year-olds; 25.6% 9-year-olds; 16.2% 10-year-olds; and 9.4% 10+ year-olds. In August the great majority (68.1-86.8%) of rookery males are 6-8 year olds. The reason for this turnover is that when older territorial bulls, present at the beginning of the breeding season, were fully spent and left shore, their territories were then occupied by younger bulls which had arrived later. On the whole, territorial tenure is brief and differs by age group with males age 9 years having the longest mean tenure (Table 6, row 3). On average, territorial tenure lasts about 15 days for bulls of age 8 years and greater (the greatest individual tenure is more than 50 days). Therefore, harem bulls change at least twice during the main reproductive period, and not less than 3-4 times during the whole reproductive season 10 June to the end of August.

On average the reproductive life of bulls lasts only 1.6 seasons, about the same as in the Pribilof herd (Johnson 1968). The majority (56.6%) of bulls take part in reproduction during only one season, 32.5% during two seasons, 8.4% during three seasons, and only 2.5% are able to participate in breeding during four seasons. To estimate the reproductive effort of males in each age group, we calculated for the 1981 season the percent of the total reproductive bull-days accounted for by males of each age group (total 337 males). Males of age 8 and 9 years play the dominant role in reproduction, accounting for a total of 65.5% of the bull-days.

In 1979-81, observations of 337 tagged bulls age 7 years and older showed that 52.5% not only did not hold territories on the rookery, they did not even make such attempts. Instead, they passed the whole summer on the bachelor grounds. The proportion of such nonbreeding individuals is greatest (> 80%) for 7-year-olds. Some nonbreeders are too small to compete with fully grown bulls, and will begin reproducing at an older age. Nevertheless, about 30% of males aged 8 years and older are "reproductively neutral" individuals which will take no part in reproduction during their entire lives. This group, which involves the same individuals over time, has a greater mortality rate than for "reproductively active" males; by age 12 years most of this group has died. This phenomenon should be considered when assessing the number of bulls necessary to maintain normal reproductive processes.

DISCUSSION

Urilie rookery is relatively unaffected by human activities. Thus, our results best characterize populations that are living under close to natural conditions. Some of our values, such as the proportions of male age classes residing on shore, will probably be higher in exploited populations. The results of this study on age structure suggest that all existing mathematical models of fur seal population dynamics need to be reviewed and made more precise, and that significant corrections should be made in the present assessment and prognostic methods.

The data on female age composition and pregnancy rate by age suggest that recruitment of young females aged 5-7 years into the reproductive process is one of the main factors causing variations in the number of pups born. An analogous conclusion was reached by Kuzin and Panina (1977) based on data from Robben Island. These relationships must be incorporated into long-term population models.

Because the fluctuations of 8-year-old bulls and of young females sometimes correlated well with the number of pups born, the number of bulls of age 8 may be connected in some way to the efficiency of reproduction in young females. This hypothesis needs further study.

The greater the percentage of mature females aged 3-4 years that arrive on the rookery in August and the first half of September, the greater the excess of "reproductively active" bulls (in principle) which, however, do not breed during the main harem season. This problem needs to be studied more thoroughly because it is directly connected to the principles of regulating bull numbers and the limits of the commercial kill.

The reasons why 30% of males aged 8 years and older do not participate in breeding are not yet clear. Nevertheless, the results testify to a considerable functional heterogeneity in reproductive activity of different age bulls.

With the present age structure of the herd, 7-year-old bulls play little role in reproduction during the peak month (25 June-25 July). But if the number of adult bulls were critically depressed, for example through increased harvesting of bachelors in previous years, the participation in reproduction of 7-year-old bulls would probably increase.

Actual data lead us to the conclusion that the maximum reproductive ratio between mature, breeding bulls and potentially mature females is 1:20. This ratio is based on females that are ashore from 25 June to 25 July and males that are reproductively active at age 8 and older; the ratio is specific to a population that is under almost natural conditions. This ratio should be central to every calculation concerning optimization of the age-sex structure of the fur seal herd which has the space and other conditions necessary to grow.

The data presented here are undoubtedly still preliminary because our limited sample makes it difficult to judge the regularity and age dynamics of reproduction. Nevertheless, the data give us some understanding of this aspect of reproduction that was until now poorly studied. Further investigations will make it possible to precisely assess reproduction in fur seal populations.

CONCLUSIONS

Our investigations on Urilie rookery give the following conclusions on the optimum or near-optimum age-sex structure of fur seals:

1. A clear correlative dependence is observed between the number of fur seal pups born and the summed percent of females age 5-7 and >15 years that arrive 25 June-25 July. These females account for more than 30% of the pups born.

2. The average birth rate among females which concentrate on the rookery in June-July is 82.4%.

3. Almost 57% of mature females give birth annually to a pup. The remainder occasionally miss pregnancy in one year, but no females were found that consistently lacked pups.

4. The overwhelming majority of pregnant females arrive 25 June-25 July, that is, during the main breeding period.

5. By 31 July, 98.4% of females age 7 and older have arrived. The percentage of younger females arriving decreases progressively depending on age (Table 3).

6. Among females age 4-5 years that are ashore in June-July, 72.5-77.8% are pregnant.

7. Nonpregnant females age 3-5 years, both mature and immature, arrive and breed in August to mid-September, after the majority of breeding has ended. Thus the breeding season is longer than previously believed.

8. The arrival of new bulls to the rookery is greatest (63.1% of those 7+ years) in June and is virtually ended by the end of July.

9. The age structure of breeding males becomes progressively younger throughout the summer-autumn season. In July, 8- and 9-year-olds predominate (55-60%).

10. Territorial tenure on breeding areas increases in bulls up to age 9 and then decreases (Table 7). Tenures suggest two complete changes of males during the main breeding period, and three to four changes from June-August.

11. Males at age 8 and 9 contribute most (65.5%) of the bull-days of reproductive effort.

12. About 30% of bulls 8 years old and older are distributed on bachelor grounds and do not attempt to establish a territory during the breeding season.

13. A correlation sometimes exists between the relative number of bulls age 8 in the main reproductive group and the number of pups born the next year.

14. The mean number of fur seal females inseminated by one reproductively active male at age 8 and older is about 20.

ACKNOWLEDGMENTS

I am very grateful to R. L. Gentry for his kind assistance in preparing and editing the English version of this paper.

CITATIONS

ANDREEV, V. L., T. I. BULGAKOVA, and F. G. CHELNOKOV.
1978. The assessment method of some parameters of the fur seal populations according to the materials of the tagging. Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. (VNIRO) 128:23-32.

BARTHOLOMEW, G. A., and L. G. HOEL.
1953. Reproductive behavior of the Alaska fur seal. Mammalia 34:417-436.

BIGG, M. A.
1979. Preliminary comments on pregnancy rate and age at first pupping in northern fur seals. *In* Kajimura, H., R. H. Lander, M. A. Perez, A. E. York, and M. A. Bigg (eds.), Preliminary analysis of pelagic fur seal data collected by the United States and Canada during 1958-74, p. 123-142. Manuscr. rep. submitted to 22nd Annu. Meet., Stand. Sci. Committee, N. Pac. Fur Seal Comm., Wash., D.C. Avail. Natl. Mar. Mamm. Lab., Seattle, WA 98115.

BORODIN, R. G., and V. A. VLADIMIROV.
1975. To the assessment of the modern condition of the Commander fur seal population. *In* Commercial ichthyology, Ser. 1, no. 7, p. 7-8, TSNIITEIRH.

BULGAKOVA, T. I.
1972. The estimation of the optimum balanced kill of the fur seals inhabiting Robben Island. *In* Theses of the reports of the All-Union Meeting on the Studying of Marine Mammals, p. 7-13. Makhachkala, USSR.
1973. The application of the mathematical models to the estimation of the optimal balanced killing of fur seals on Robben Island. Tr. TSNIITEIRH, ser. Commercial Fisheries 2:39-52.

BYCHKOV, V. A.
1964. Observations of female fur seals on Robben Island. Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. (VINRO)-Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. (TINRO) 51-54:91-96.
1969. The composition and the distribution of female fur seals on the harem rookery of Robben Island. *In* Marine mammals, p. 75-82. Moscow.

CHAPMAN, D. G.
1964. A critical study of Pribilof fur seal population estimates. Fish. Bull., U.S. 63:657-669.
1973. Spawner-recruit models and estimation of the level of maximum sustainable catch. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 1964:325-332.

CHELNOKOV, F. G.
1977. The forecasting of the bachelors sealing and the population dynamics of the fur seal bulls on the south-eastern rookery of Medney Island. *In* Marine mammals of the Pacific Ocean, no. 1, p. 18-34, Vladivostok.

CRAIG, A. M.
1964. Histology of reproduction and estrus cycle in the female fur seal. J. Fish. Res. Board Can. 21:773-811.

EBERHARDT, L. L.
1981. Population dynamics of the Pribilof fur seals. *In* Fowler, C.W., and T. D. Smith (eds.), Dynamics of large mammal populations, p. 197-220. Wiley and Sons, N.Y.

ICHIHARA, T.
1971. Maximum sustainable yield in the Robben Island fur seal herd. Proc., XIV Annu. Meet. N. Pac.Fur Seal Comm., Wash., D.C.

JOHNSON, A. M.
1968. Annual mortality of territorial male fur seals and its management significance. J. Wildl. Manage. 169:94-99.

KOLESNIK, Yu. A., and V. M. KOGAY.
1977. Methods of the determination of the fur seal number. *In* Marine mammals of the Pacific Ocean, no. 1, p. 41-45, Vladivostok.

KUZIN, A. E., and G. K. PANINA.
1977. Age-sex structure and the reproductive capacity of the fur seal population on Robben Island. *In* Investigations on fish biology and commercial oceanography, no. 8, p. 98-105, Vladivostok.

LANDER, R. H.
1975. Method of determining natural mortality in the northern fur seal, *Callorhinus ursinus*, from known pups and kill by age and sex. J. Fish. Res. Board Can. 32:2447-2452.
1979. Role of land and ocean mortality in yield of male Alaskan fur seal, *Callorhinus ursinus*. Fish. Bull., U.S. 77:311-314.
1981. A life table and biomass estimate for Alaskan fur seals. Fish. Res. (Amst.) 1:55-70.

NAGASAKI, F.
1961. Population study on the fur seal herd. Spec. publ. 7, Tokai Reg. Fish. Res. Lab., p. 1-60.

NESTEROV, G. A.
1978. Determination of the value of the fur seals born according to the females number on a rookery. *In* Marine mammals, p. 244-245. TSNIITEIRH, Moscow.

NORTH PACIFIC FUR SEAL COMMISSION.
1981. Report on investigations for 1973-76. [in Russian]. Hyattsville, MD, 197 p.
SKALETSKAYA, E. I., E. Ja. FRISMAN, and A. E. KUZIN.
1980. Estimation of the population dynamics of the northern fur seals. Reprint no. 11, IAPU DVNTS AN SSSR, Vladivostok.
SMITH, T. D., and T. POLACHECK.
1981. Reexamination of the life table for northern fur seals with implication about population regulatory mechanism. *In* Fowler, C. W., and T. D. Smith (eds.), Dynamics of large mammal populations, p. 99-120. Wiley and Sons, N.Y.
TIMOFEEVA, A. A., T. I. CHUPAHINA, and Yu. A. KOLESNIK.
1977. To the problem on the determination of the fur seals number on Robben Island. *In* Marine mammals of the Pacific Ocean, no. 1, p. 35-40, Vladivostok.
VLADIMIROV, V. A., et al.
1979. Investigations on fur seals conducted by the Soviet Union in 1978. ONTI, Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. (VNIRO), Moscow, 95 p.
VLADIMIROV, V. A.
1978. Population status of stock fur seals of Tyuleniy Island. Zool. Zh. 57(8): 1239-1249. (In Russ., Engl. summary)
1982. On the possibility of determining the newly born fur seal pups number according to the age composition of the fur seal females. Proc. XXV Meet. N. Pac. Fur Seal Comm., Doc. NPFSC/WS/82/USSR.
VLADIMIROV, V. A., N. N. LYSKIN, and V. N. SADOVOV.
1982. Some results of the investigations of the northern fur seals biology on the Urylie rookery of Medny Island, 1978-1981. Dep. Sci. Tech. Inf., Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. (VNIRO), Moscow, p. 58.
YORK, A. E.
1979a. Analysis of pregnancy rates of female fur seals in the combined United States-Canadian pelagic collections, 1958-1974. *In* Kajimura, H., R. H. Lander, M. A. Perez, A. E. York, and M. A. Bigg (eds.), Preliminary analysis of pelagic fur seal data collected by the United States and Canada during 1958-74, p. 50-122. Manuscr. rep. submitted to 22nd Annu. Meet., Stand. Sci. Committee, N. Pac. Fur Seal Comm., Wash., D.C. Avail. Natl. Mar. Mamm. Lab., Seattle, WA 98115.
1979b. Pregnancy rates and migration. *In* Kajimura, H., R. H. Lander, M. A. Perez, A. E. York, and M. A. Bigg (eds.), Preliminary analysis of pelagic fur seal data collected by the United States and Canada during 1958-74, p. 58-63. Manuscr. rep. submitted to 22nd Annu. Meet., Stand. Sci. Committee, N. Pac. Fur Seal Comm., Wash., D.C. Avail. Natl. Mar. Mamm. Lab., Seattle, WA 98115.
1983. Average age at first reproduction of the northern fur seal. Can. J. Fish. Aquat. Sci. 40:121-127.
YORK, A. E., and J. R. HARTLEY.
1981. Pup production following harvest of female northern fur seals. Can. J. Fish. Aquat. Sci. 38:84-90
YOSHIDA, K.
1982. Study for reproductive mechanism of fur seal of Asian origin. Far Seas Fish. Lab., Bull. 20, 36 p.

Skull Morphometrics of Male Antarctic and Subantarctic Fur Seals, *Arctocephalus gazella* and *A. tropicalis*, and Their Interspecific Hybrids

GRAHAM I. H. KERLEY[1]
Mammal Research Institute
University of Pretoria
Pretoria 0002
South Africa

TERRENCE J. ROBINSON
Mammal Research Institute
University of Pretoria
Pretoria 0002
South Africa

ABSTRACT

The skull morphology of a sample of adult male subantarctic fur seals, *Arctocephalus tropicalis*, from Marion Island, antarctic fur seals, *A. gazella*, from Marion Island and South Georgia, and interspecific hybrids from Marion Island was compared. Individual variation was found to be high, and 19 variables were included in the statistical analyses. Phenograms were generated based on both the distance and correlation matrices and showed good separation between the two species. In the principal component analyses, the first component (size) accounted for 81.36% of the variation, while the second component (shape) contributed a further 3.52% of the variation. The two species separated well on the two-dimensional projection of the first two components, with the putative hybrids plotting between the two species clusters. Species integrity was tested using an *a priori* discriminant function analysis which confirmed all classifications as correct.

INTRODUCTION

The subantarctic and antarctic fur seals were considered conspecific by King (1959a,b), with *Arctocephalus tropicalis tropicalis* occurring on islands north of the Antarctic Convergence, and *A. t. gazella* on islands south of the Convergence. However, they are now accorded species status, based on cranial and dental characteristics (Repenning et al. 1971) and show external features distinct from each other. Although exploited to the verge of extinction in the last century, their recovery subsequent to the cessation of sealing has been well documented (see Bonner 1981 for a review), with the largest populations of *A. tropicalis* and *A. gazella* occurring at Gough Island and South Georgia, respectively (Bonner 1981). Concomitant with these population increases, an expansion of their breeding range took place, both species now coexisting on some islands situated near the Antarctic Convergence (Kerley 1984).

The first possible record of *A. gazella* at Marion Island was a skull collected by Rand in 1951-52 which King (1959a) identified as resembling the southern population. In 1974 Condy (1978) recorded *A. gazella* breeding sympatrically with *A. tropicalis* on the Prince Edward Islands. Since some adult male fur seals at Marion Island showed external characteristics of both species and some breeding harems contained both *A. tropicalis* and *A. gazella*, Condy (1978) speculated that hybridization was occurring between the species, although there appeared to be a degree of ecological and behavioral separation.

The present study was initiated to investigate the relationships between these two species at the Prince Edward Islands. To date, information has been presented on the assessment of population sizes and trends and the extent of hybridization (Kerley 1983a), comparison of seasonal haulout patterns (Kerley 1983b), and a comparison of pup growth (Kerley 1985). This report presents the results of univariate and multivariate analyses of skull morphology of specimens of *A. tropicalis*, *A. gazella*, and the putative hybrids.

MATERIALS AND METHODS

Species identification in the field relied on external characteristics following Bonner (1968) and Condy (1978). Skulls of 47 fur seals, *Arctocephalus* spp. (Table 1), were examined and 34 cranial measurements recorded for each specimen. Measurements were taken to the nearest 0.1 mm with a vernier caliper, except for the facial angle measurement (Repenning et al. 1971) which was taken to the nearest degree with an engineer's protractor. Measurements used corresponded to those used in other otariid studies (Sivertsen 1954; King 1959a; Orr et al. 1970; Repenning et al. 1971). External body measurements, which were available only for the Marion Island specimens, were excluded from the analyses. Since fur seals

Table 1—Reference numbers, species, source localities, and sample sizes for the *Arctocephalus* specimens used in this study.

Reference no. (OTU's)	*Arctocephalus* species	Source locality	*n*
1 - 15	*A. gazella*	S. Georgia	15
16 - 19	*A. gazella*	Marion I.	4
20 - 42	*A. tropicalis*	Marion I.	23
43 - 47	Hybrid	Marion I.	5

[1]Present address: Department of Zoology, University of Port Elizabeth, P. O. Box 1600, Port Elizabeth 6001, South Africa.

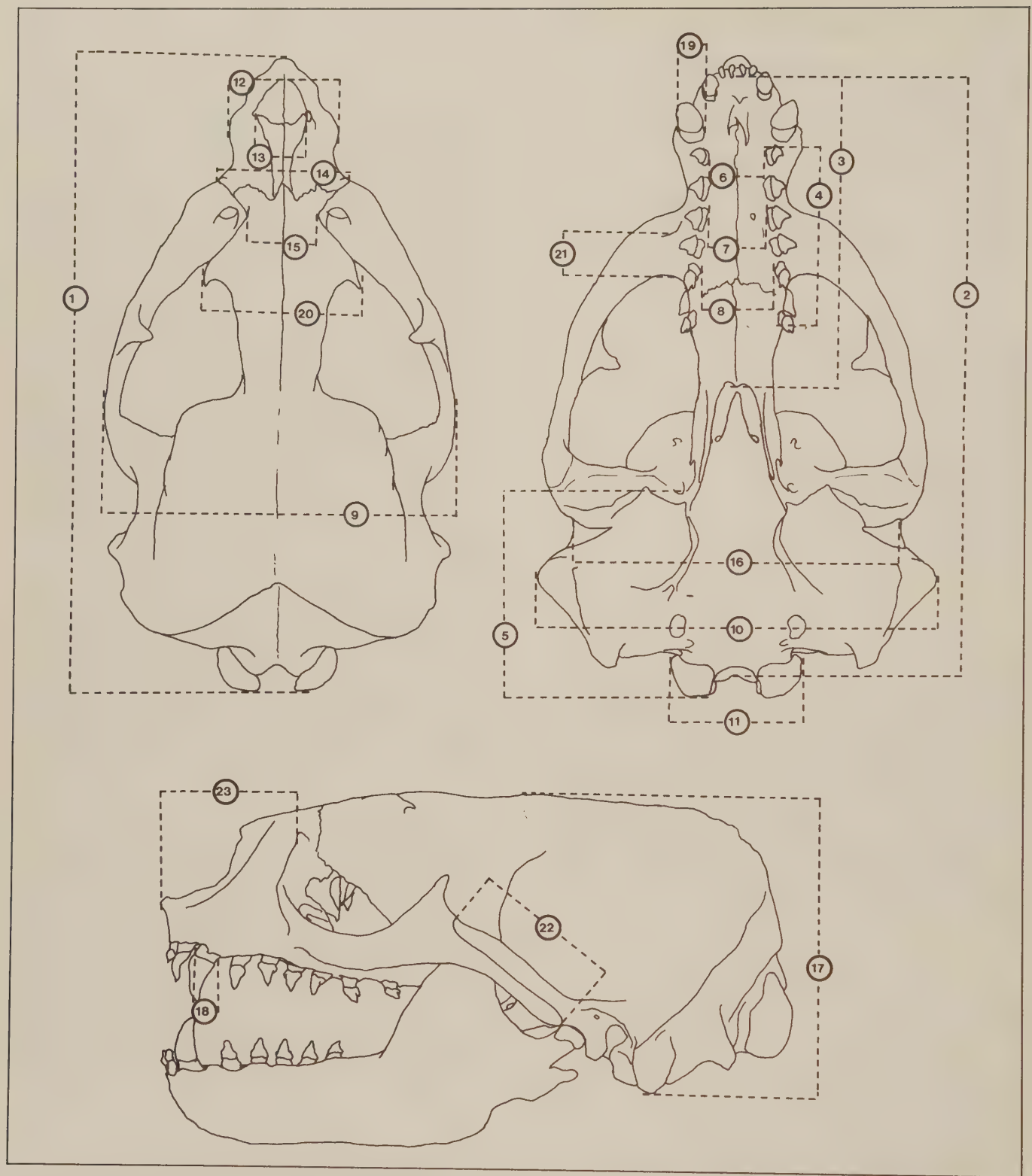


Figure 1—Diagrammatic representation of 19 variables utilized in the present study, as well as the four variables (20-23) previously used to differentiate between *Arctocephalus tropicalis* and *A. gazella* but excluded from the present study. 1 = condylobasal length; 2 = basilar length of Hensel; 3 = palital length; 4 = upper postcanine length; 5 = optic foramen-condyl length; 6 = palate width at molar 1; 7 = palate width at molar 3; 8 = palate width at molar 5; 9 = zygomatic width; 10 = mastoid width; 11 = occipital condyl width; 12 = rostral width; 13 = maximum nasal width; 14 = preorbital process width; 15 = interorbital process width (ant.); 16 = calvarial width; 17 = skull height (at tympanic bulla); 18 = canine diameter (lengthwise); 19 = canine diameter (widthwise); 20 = supraorbital process width; 21 = zygomatic root width; 22 = squamosal-jugal suture length; 23 = gnathion to preorbital process length.

exhibit sexual dimorphism with adult males commonly more than twice the size of adult females (Bonner 1981), this source of variation was excluded by including only males in this study. A second source of variation, that of age, was reduced by using only adult specimens. Sivertsen's (1954) suture index was used for aging, and only specimens with an index of 19 or more—corresponding to an age of 8 years or older (M. N. Bester, Univ. Pretoria, pers. commun.)—were included in the analyses.

Measurement trials for both species were carried out for all the cranial measurements (five repetitions, $n=5$), and all measurements were found to be highly repeatable. Individual variation, as expressed by the coefficient of variation (CV), was determined for all variables. The operational taxonomic units (OTU's) for the analyses were individual specimens.

Univariate analyses yielding standard statistics (mean, range, standard deviation, standard error, variance, among others) were performed using the CONDESCRIPTIVE subprogram of the Statistical Package for Social Sciences (SPSS; Statistical Package for Social Sciences 1983).

The Marion Island and South Georgia *A. gazella* subsamples were tested for significant differences using the ONEWAY subprogram of the SPSS package. This is a single classification analysis of variance (ANOVA).

Multivariate statistical analyses were performed using selected subroutines of the Numerical Taxonomy System of Multivariate Statistical Programs (NT-SYS; Rohlf et al. 1974). Matrices of Pearson's product-moment correlation and taxonomic distance coefficients were computed. Cluster analyses were performed utilizing the unweighted pair group method with arithmetic averages (UPGMA) on the correlation and distance matrices. Phenograms were generated for both. The NT-SYS principal component analysis (PCA) allows an objective assessment of data without prior grouping of material.

The PCA is based on correlation coefficients among characters. Two-dimensional projections of the pairwise comparisons of the first three components generated by the program were analyzed. Factor matrices indicating the character loadings in these components and the percentage of variation accounted for by them were computed. A minimum spanning tree (MST) was superimposed on the two-dimensional projections of the PCA. This shows the affinities of the OTU's to each other and indicates the degree of distortion created by representing the OTU's in a two-dimensional projection.

Two-group discriminant function analysis using the DISCRIMINANT subprogram of the SPSS package was used for checking species integrity. Discriminant analysis is a statistical technique in which linear combinations of variables are used to distinguish between two or more categories of cases (OTU's). The criterion for controlling the stepwise selection of variables was the minimum Wilks Lambda. The variables "discriminate" between groups of cases and predict into which category or group a case falls, based upon the values of these variables. A two-group analysis was used since this allows discrimination between *A. tropicalis* and *A. gazella* as well as between these two species and their interspecific hybrids.

A review of the theory, underlying assumptions, and methods of multivariate analyses for systematics is given by Neff and Marcus (1980). Computer analyses using the NT-SYS and SPSS packages were conducted on the University of Pretoria IBM 370 computer.

RESULTS

Individual variation

Individual variation, as expressed by the coefficient of variation (CV), was determined for all 34 variables and found to be relatively high. Nineteen variables (Fig. 1, Table 2) with relatively low variation (CV<8.0) or little or no interspecific overlap were included in the analyses. Of the ten variables considered by King (1959a) and Bonner (1968) to differentiate between *A. tropicalis* and *A. gazella*, four were excluded from the analyses because these variables exhibited either high individual variation or species overlap or both (Table 3).

Geographic variation in *A. gazella*

Analyses of variance showed that the Marion Island and South Georgia *A. gazella* samples differed significantly in only 6 of the 19 variables (Table 4). This is probably due to the presence of two small individuals in the Marion Island sample, as well as the small sample size. These two individuals, however, were both adults (OTU 16 suture index = 19; OTU 17 suture index = 20) and possibly represent the lower limit of the adult size range. Both were retained and the two sample localities were combined for further analyses.

Species delimitation

The values for *A. gazella* of all 19 variables were greater than those for *A. tropicalis*, with the interspecific hybrids having intermediate values (Table 2). Phenograms showing the interspecific relationships between the two species were computed from both the distance and correlation matrices.

The distance phenogram, with a cophenetic correlation coefficient of 0.782, clearly shows the separation of the two species (Fig. 2). Two major clusters are evident, A and B. Major cluster B, grouped relatively tightly, comprises all of the *A. tropicalis* specimens. Major cluster A comprises all of the *A. gazella* specimens as well as the interspecific hybrids and is further divided into subclusters C and D. The single *A. gazella* specimen forming subcluster D (OTU 10) is an extremely large specimen whose measurements formed the upper limit of the *A. gazella* range in 14 of the 19 variables (74%). Subcluster C subdivides into sections E and F. Subdivision E comprises the larger *A. gazella* specimens (condylobasal lengths $\geqslant$ 237.2 mm, mean = 242.3 mm, n = 16, range = 237.2-253.4) as well as the largest hybrid (OTU 44, CBL = 247.4 mm). Subdivision F comprises the two small *A. gazella* specimens mentioned earlier (OTU 16, CBL = 227.7 mm; OTU 17, CBL = 228.4 mm) as well as the other four interspecific hybrids.

The correlation phenogram with a low cophenetic correlation coefficient of 0.534 did not separate the taxa, and since no clear pattern was discernable in the placement of the OTU's, the phenogram has not been presented in the text.

The results of the principal component analysis are given in Table 5 as well as Figures 3 and 4. The first component accounts for 81.36% of the total variation and is an overall size component as suggested by the large and positive coefficients for all measurements

Table 2—Species variation in cranial morphology of *Arctocephalus tropicalis* ($n=23$), *A. gazella* ($n=19$), and their interspecific hybrids ($n=5$).

Variable and species	Mean (mm)	SE	CV (%)	Range (mm)
Condylobasal length				
A. tropicalis	217.0	1.35	2.98	206.3-228.6
A. gazella	241.5	1.77	3.19	227.7-255.5
hybrid	231.5	4.51	4.36	221.3-247.4
Basilar length of Hensel				
A. tropicalis	194.8	1.21	2.97	185.3-204.0
A. gazella	217.7	1.57	3.14	207.3-230.9
hybrid	208.5	4.14	4.44	197.4-221.5
Palital length				
A. tropicalis	94.5	0.81	4.11	89.2-103.0
A. gazella	113.1	1.54	5.94	94.2-124.4
hybrid	103.4	2.70	5.84	93.8-109.2
Upper postcanine length				
A. tropicalis	57.6	0.58	4.83	51.6-62.6
A. gazella	64.8	0.78	5.23	57.9-70.4
hybrid	61.7	2.16	7.80	54.3-66.2
Optic foramen - condyl length				
A. tropicalis	98.4	0.67	3.26	93.1-105.1
A. gazella	108.3	0.99	3.99	102.8-119.6
hybrid	105.7	2.08	4.39	98.1-110.4
Palate width - molar 1				
A. tropicalis	22.3	0.35	7.55	19.2-25.5
A. gazella	28.7	0.50	7.62	23.7-33.4
hybrid	26.4	0.59	5.00	24.9-28.3
Palate width - molar 3				
A. tropicalis	23.4	0.42	8.59	20.5-27.8
A. gazella	31.3	0.46	6.46	27.8-36.7
hybrid	29.1	0.79	6.05	26.1-30.7
Palate width - molar 5				
A. tropicalis	28.2	0.55	9.26	23.6-33.5
A. gazella	40.9	0.80	8.50	35.3-51.1
hybrid	36.9	1.24	7.51	33.7-39.6
Zygomatic width				
A. tropicalis	133.0	1.15	4.13	122.3-142.8
A. gazella	147.5	1.92	5.67	132.2-167.3
hybrid	147.2	3.90	5.92	138.6-161.9
Mastoid width				
A. tropicalis	123.5	1.10	4.28	115.9-135.3
A. gazella	138.1	2.52	7.97	112.9-164.6
hybrid	134.7	3.29	5.46	127.4-146.1
Occipital condyl width				
A. tropicalis	48.3	0.43	4.23	44.5-51.8
A. gazella	54.2	0.75	5.99	47.6-59.8
hybrid	51.3	1.10	4.79	49.0-54.4
Rostral width				
A. tropicalis	43.6	0.61	6.70	38.1-49.5
A. gazella	56.9	1.02	7.78	49.7-65.3
hybrid	50.2	0.80	3.56	48.9-53.1
Maximum nasal width				
A. tropicalis	26.3	0.46	8.29	22.7-29.9
A. gazella	33.1	0.45	5.96	29.3-36.5
hybrid	31.0	0.80	5.76	28.8-32.9
Preorbital process width				
A. tropicalis	50.4	0.67	6.40	45.2-56.6
A. gazella	65.5	0.76	5.09	57.4-74.1
hybrid	61.0	1.18	4.32	56.9-63.6
Interorbital process width (anterior)				
A. tropicalis	22.0	0.46	10.04	17.5-25.9
A. gazella	36.9	0.65	7.72	32.5-42.3
hybrid	32.7	1.58	10.81	27.5-35.9
Calvarial width				
A. tropicalis	106.6	0.87	3.92	98.6-113.1
A. gazella	117.4	1.44	5.36	107.9-135.4
hybrid	116.4	4.21	8.09	105.4-131.4
Skull height (at bulla)				
A. tropicalis	86.6	0.88	4.86	77.5-95.0
A. gazella	99.2	1.34	5.88	87.6-110.9
hybrid	95.5	1.46	3.42	91.8-99.5
Canine diameter (lengthwise)				
A. tropicalis	11.1	0.19	8.10	9.7-13.4
A. gazella	14.2	0.19	5.74	13.2-16.5
hybrid	12.2	0.69	12.60	10.1-14.1
Canine diameter (widthwise)				
A. tropicalis	9.3	0.17	8.82	7.7-11.0
A. gazella	12.1	0.22	8.00	10.9-14.8
hybrid	10.5	0.45	9.69	9.1-11.7

Table 3—Species variation in four cranial variables previously used to differentiate *Arctocephalus tropicalis* and *A. gazella* (King 1959a, Bonner 1968) but excluded from the present study.

Variable and species	Mean (mm)	SE	CV (%)	Range (mm)
Supraorbital process width				
A. tropicalis	48.7	1.18	11.59	39.3-57.1
A. gazella	63.3	1.53	10.53	53.7-75.0
Zygomatic root width				
A. tropicalis	13.3	0.39	13.92	9.7-18.3
A. gazella	19.9	0.34	7.42	16.5-22.2
Squamosal-jugal suture length				
A. tropicalis	39.9	0.51	6.23	36.4-45.6
A. gazella	34.0	1.04	13.37	23.4-43.5
Gnathion to preorbital process length				
A. tropicalis	48.2	0.800	8.00	37.7-54.9
A. gazella	57.5	0.72	5.47	50.8-62.5

Table 4—Geographic variation in cranial morphology of *Arctocephalus gazella* from Marion Island (MI, $n=4$) and South Georgia (SG, $n=15$). Underlined variables differ significantly ($P < 0.05$).

Variable and locality	Mean (mm)	SE	CV (%)	Range (mm)	Probability
Condylobasal length					
MI	233.4	3.14	2.69	227.7-240.2	0.01
SG	243.7	1.71	2.72	234.9-255.5	
Basilar length of Hensel					
MI	211.6	2.42	2.28	207.3-218.4	0.04
SG	219.4	1.66	2.93	210.2-230.9	
Palital length					
MI	106.7	4.63	8.68	94.2-114.0	0.03
SG	114.9	1.28	4.33	105.5-124.4	
Upper postcanine length					
MI	63.4	1.36	4.29	60.2-66.6	0.34
SG	65.2	0.91	5.40	57.9-70.4	
Optic foramen - Condyl length					
MI	105.1	0.62	1.17	103.7-106.7	0.10
SG	109.1	1.15	4.10	102.8-119.6	
Palate width - molar 1					
MI	28.4	1.22	8.61	25.6-31.3	0.77
SG	28.8	0.57	7.64	23.7-33.4	
Palate width - molar 3					
MI	31.8	1.11	6.95	28.8-34.0	0.61
SG	31.2	0.53	6.52	27.8-36.7	
Palate width - molar 5					
MI	40.2	1.19	5.91	37.3-42.6	0.64
SG	41.1	0.97	9.14	35.3-51.1	
Zygomatic width					
MI	145.1	5.02	6.91	132.2-153.7	0.54
SG	148.2	2.10	5.50	135.3-167.3	
Mastoid width					
MI	128.7	6.04	9.39	112.9-138.8	0.05
SG	140.6	2.48	6.83	128.1-164.6	
Occipital Condyl width					
MI	53.1	0.84	3.16	51.0-54.7	0.42
SG	54.6	0.91	6.47	47.6-59.8	
Rostral width					
MI	56.7	3.35	11.83	49.7-64.3	0.94
SG	56.9	1.02	6.93	52.6-65.3	
Maximum nasal width					
MI	31.1	0.83	5.31	29.3-33.3	0.02
SG	33.6	0.45	5.17	31.0-36.5	
Pre-orbital process width					
MI	61.6	1.70	5.52	57.4-65.3	0.01
SG	66.5	0.66	3.83	64.0-74.1	
Interorbital process width (anterior)					
MI	36.5	2.23	12.25	32.5-40.8	0.74
SG	37.0	0.64	6.66	33.6-42.3	
Calvarial width					
MI	112.4	2.28	4.06	107.9-117.7	0.07
SG	118.8	1.57	5.13	110.8-135.4	
Skull height (at bulla)					
MI	95.5	4.08	8.56	87.6-102.5	0.15
SG	100.2	1.27	4.92	92.7-110.9	
Canine diameter (lengthwise)					
MI	14.3	0.47	6.61	13.2-15.5	0.89
SG	14.2	0.21	5.74	13.5-16.5	
Canine diameter (widthwise)					
MI	12.7	0.83	13.06	11.0-14.8	0.27
SG	12.0	0.19	6.14	10.9-13.3	

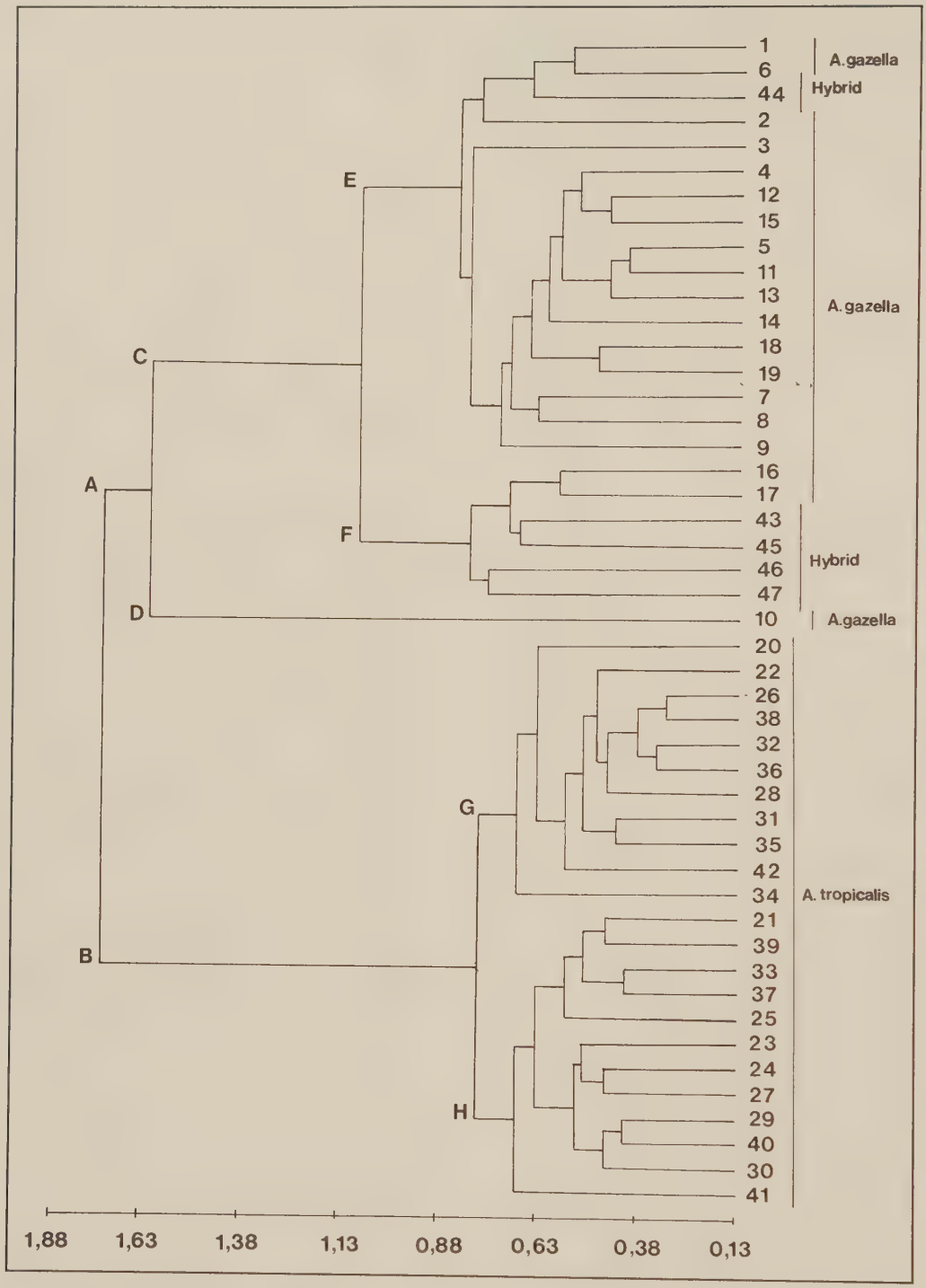


Figure 2—Distance phenogram of specimens of *Arctocephalus tropicalis*, *A. gazella*, and the interspecific hybrid clustered by the unweighted pair-group method using arithmetic averages. Cophenetic correlation coefficient = 0.782. Numbers refer to OTU's.

Table 5—Factor matrix from the 19-variable principal component analysis of specimens of *Arctocephalus gazella*, *A. tropicalis*, and the interspecific hybrid, showing the character loadings on the first three components.

Variable	Factor I	Factor II	Factor III
Condylobasal length	0.947	0.020	−0.176
Basilar length of Hensel	0.940	−0.004	−0.173
Palital length	0.924	−0.093	−0.078
Upper postcanine length	0.800	−0.132	−0.254
Optic foramen - condyl length	0.891	0.053	−0.165
Palate width - molar 1	0.946	0.094	0.167
Palate width - molar 3	0.918	−0.003	0.215
Palate width - molar 5	0.939	−0.029	0.182
Zygomatic width	0.886	0.353	0.134
Mastoid width	0.879	0.331	−0.078
Occipital condyl width	0.806	−0.045	−0.440
Rostral width	0.957	−0.095	0.082
Maximum nasal width	0.881	−0.155	0.160
Pre-orbital process width	0.949	−0.021	0.177
Interorbital process width (anterior)	0.936	−0.119	0.179
Calvarial width	0.863	0.339	−0.067
Skull height (at bulla)	0.930	0.126	0.008
Canine diameter (lengthwise)	0.844	−0.393	−0.040
Canine diameter (widthwise)	0.879	−0.246	0.068

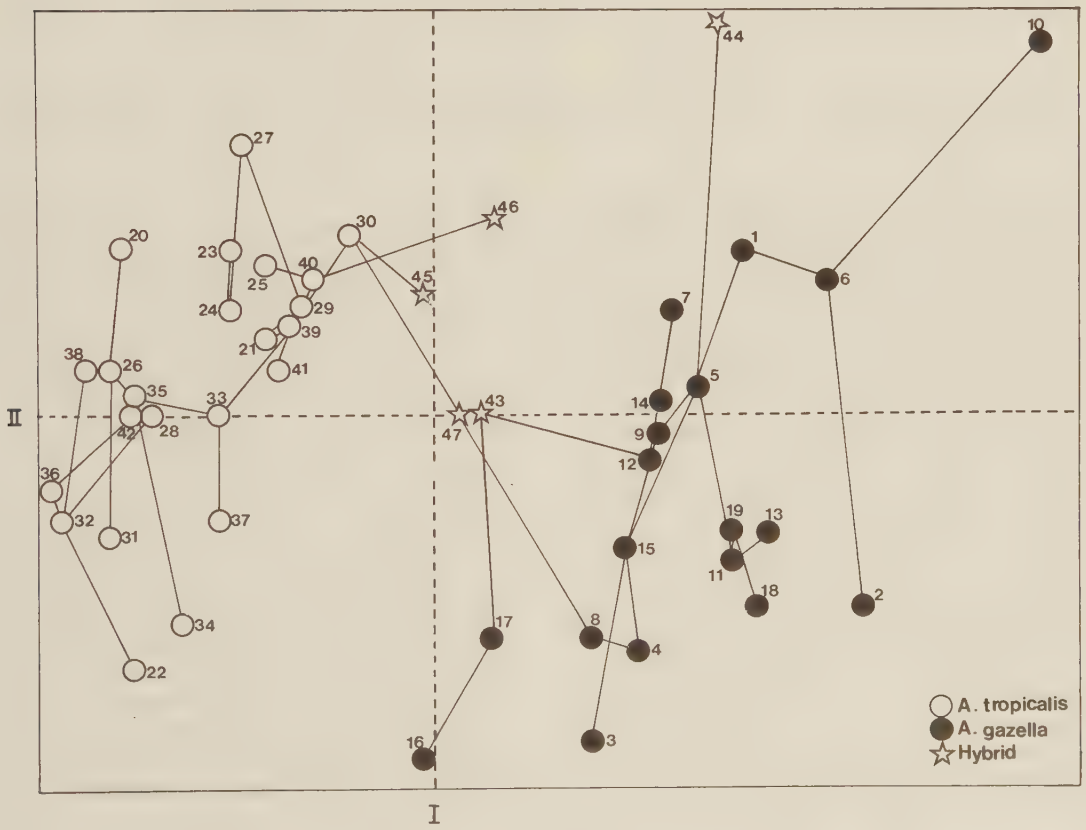


Figure 3—Pairwise comparison of factors I and II from the principal component analysis of the *Arctocephalus* specimens. Numbers refer to OTU's.

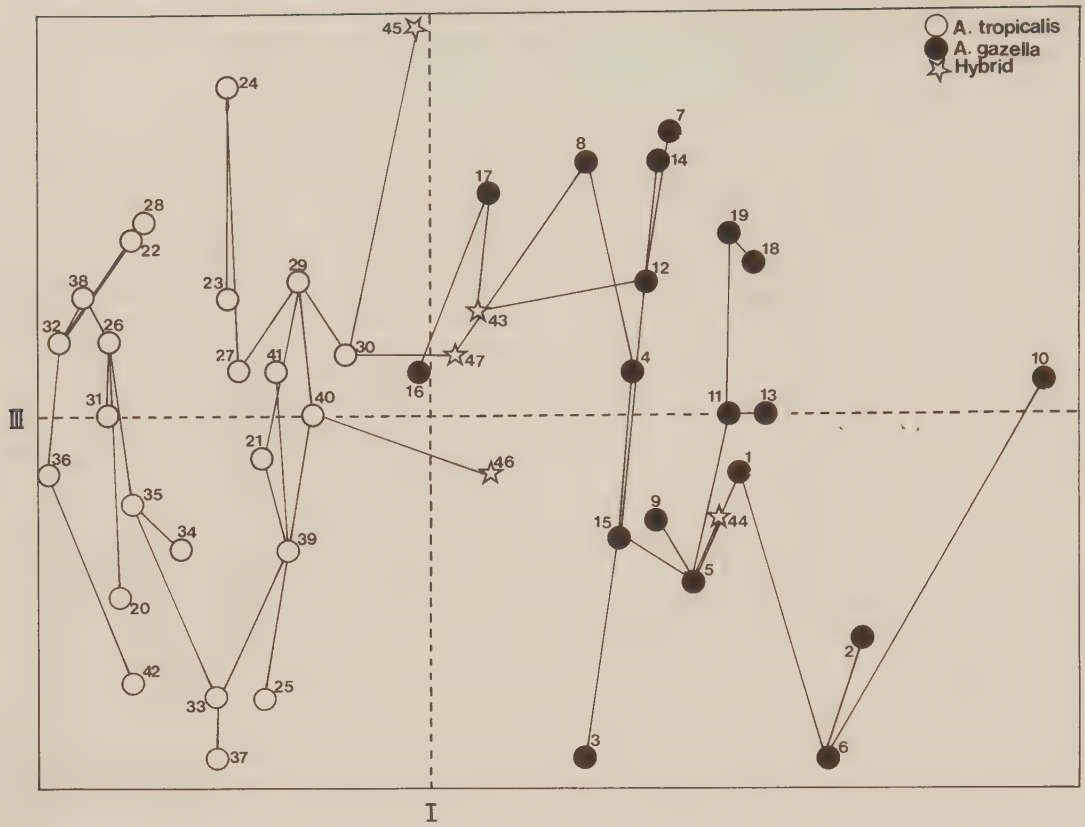


Figure 4—Pairwise comparison of factors I and III from the principal component analysis of the *Arctocephalus* specimens. Numbers refer to OTU's.

(Table 5). The second, which accounts for an additional 3.52% of the trace, is a shape component since the character loadings indicate that this component is influenced mostly by zygomatic, mastoid, maximum nasal, and calvarial widths as well as the canine diameters (both lengthways and widthways) and the upper postcanine length. The third component which contributes an additional 3.10% to the total phenetic variation (total = 87.99%) is influenced primarily by upper postcanine length, palate width at molar 3, and occipital condyl width. Although the eigenvalues for components II and III are less than unity (0.67 and 0.59, respectively), this does not necessarily mean that they have no biological significance (N. J. Dippenaar, Transvaal Mus., Pretoria, pers. commun.).

The ordination diagram illustrating the pairwise comparison of components I and II (Fig. 3) shows good separation between the *A. tropicalis* OTU's (20-42) and the *A. gazella* OTU's (1-19) along component I, with the *A. tropicalis* OTU's clustered on the left of the component scale while the *A. gazella* OTU's cluster towards the right of the component scale. The outlying *A. gazella* OTU (10) is the large specimen mentioned earlier. The interspecific hybrid OTU's (43-46) occupy an intermediate position between the two species. The two species did not separate clearly along the second component.

In the ordination diagram illustrating the pairwise comparison of components I and III, the separation of the *A. tropicalis* and *A. gazella* OTU's along component I is repeated (Fig. 4). However, further distinction was masked by the lack of separation along the third component as was to be expected from the low contribution of this component (3.10%) towards the total phenetic variation.

The distinctiveness of the OTU's representing *A. tropicalis* and *A. gazella* is greatly enhanced by the addition of the minimum spanning tree (MST) connections to the principal component analyses ordination diagrams (Figs. 3 and 4). All of the OTU's representing the two species have nearest relative connections with the exception of the two small Marion Island *A. gazella* OTU's (16 and 17) which are connected via an interspecific hybrid (OTU 43) to the other *A. gazella* OTU's. Revealingly, the MST connection between the two species is via an interspecific hybrid (OTU 47), emphasizing the intermediate nature of the interspecific hybrids.

Discriminant function analysis

The *A. tropicalis*, *A. gazella*, and interspecific hybrid samples were compared pairwise in a two-group discriminant function analysis for the purposes of identification. The cranial variables selected by this procedure are useful for the identification of the taxa but are not necessarily the most important characters in the data set. The corresponding standardized and unstandardized coefficients and the constants are presented in Table 6. The derived discriminant scores, plotted as frequency histograms (Fig. 5), clearly illustrate the separation between the two species and between the species and the hybrids. All OTU's were correctly classified *a posteriori*.

DISCUSSION

The fur seals in this study exhibited relatively high variation (as expressed by the CV) for cranial measurements, especially when compared with skeletal measurements of bats (Swanepoel and Genoways 1978) and lagomorphs (Yates et al. 1979; Robinson and Dippenaar 1983). The CV's for skeletal measurements found here

Table 6—Results of the two-group discriminant function analysis of (a) *Arctocephalus tropicalis* and *A. gazella*, (b) *A. tropicalis* and the interspecific hybrids, and (c) *A. gazella* and the interspecific hybrids.

A. *Arctocephalus tropicalis* and *A. gazella*

Measurement	*A. tropicalis* $\bar{x}$ (mm)	*A. gazella* $\bar{x}$ (mm)	Unstandardized coefficients	Standardized coefficients
Basilar length of Hensel	194.8	217.7	−0.1058	−0.6638
Palate width at molar 1	22.3	28.7	0.2815	0.5423
Palate width at molar 3	23.4	31.3	−0.2027	−0.4086
Mastoid width	123.5	138.1	0.1503	1.2559
Preorbital process width	50.4	65.5	−0.1163	−0.3806
Interorbital process width (anterior)	22.0	36.9	−0.3724	−0.9358
Calvarial width	106.6	117.4	−0.1303	−0.6819
Skull height (at bulla)	86.6	99.2	0.1204	0.6024
Canine diameter (lengthwise)	11.1	14.2	−0.4916	−0.4239
Canine diameter (widthwise)	9.3	12.1	−0.4434	−0.3958
			Constant 32.1282	

B. *Arctocephalus tropicalis* and interspecific hybrids

Measurement	*A. tropicalis* $\bar{x}$ (mm)	Hybrid $\bar{x}$ (mm)	Unstandardized coefficients	Standardized coefficients
Palital length	94.5	103.4	−0.2483	−1.0639
Palate width at molar 1	22.3	26.4	0.4681	0.7650
Palate width at molar 3	23.4	29.1	−0.7595	−1.4986
Palate width at molar 5	28.2	36.9	−0.3032	0.8001
Mastoid width	123.5	134.7	0.1300	0.7350
Preorbital process width	50.4	61.0	0.7219	2.2678
Interorbital process width (anterior)	22.0	32.7	−0.9412	−2.3116
Canine diameter (lengthwise)	11.1	12.2	−0.5014	−0.5133
			Constant 14.7029	

C. *Arctocephalus gazella* and interspecific hybrids

Measurement	*A. gazella* $\bar{x}$ (mm)	Hybrid $\bar{x}$ (mm)	Unstandardized coefficients	Standardized coefficients
Upper postcanine length	64.8	61.7	0.4462	1.6466
Palate width at molar 1	28.7	26.4	1.3361	2.7459
Palate width at molar 5	40.9	36.9	−0.2565	−0.8622
Mastoid width	138.1	134.7	−0.2848	−2.9715
Occipital condyl width	54.2	51.3	0.4443	1.3862
Preorbital process width	65.5	61.0	1.1737	3.7747
Calvarial width	117.4	116.4	−0.2012	−1.4008
Skull height (at bulla)	99.2	95.5	−0.4715	−2.5717
Canine diameter (widthwise)	12.1	10.5	0.8168	0.8006
			Constant −56.1406	

resemble those for the external morphological measurements in the aforementioned studies, external morphological measurements varying more than skeletal measurements (Swanepoel and Genoways 1978). This variability may be a feature of marine mammals and should be borne in mind when variables are selected for analyses.

The results of the multivariate analyses performed here are in agreement with earlier findings (Repenning et al. 1971) that *A. tropicalis* and *A. gazella* are phenotypically distinct species. The two species differ principally in the size of their skulls, with *A. gazella* being larger than *A. tropicalis*. Four measurements previously used to differentiate these two species, namely supraorbital process width, zygomatic root width, squamosal-jugal suture length, and gnathion-to-preorbital process length (King 1959a; Bonner 1968) were found to be unsuitable for taxonomic purposes due to high intraspecific variation or interspecific overlap. The two species were most clearly separated in the phenogram generated from the distance matrix. No meaningful separation of OTU's resulted from the correlation phenogram. Similarly, the clearest differentiation between the two species was found along Component I (size) of the PCA ordination diagrams, with poor separation along the second and third components

In addition to the above separation between these two species, the results of the stepwise discriminant function analyses provide a highly reliable means of distinguishing these two *Arctocephalus* species. Of the 19 variables used in this study, 10 (Table 6a) provide maximum separation between adult male specimens of *A. tropicalis* and *A. gazella*. The measurements obtained for unknown specimens are multiplied by the measurements corresponding to unstandardized coefficients (Table 6a), summated, and added to the appropriate constant. The resultant discriminant score can then be plotted in the histograms of discriminant scores (Fig. 5), and the unknown will group within the species with which it has the greatest

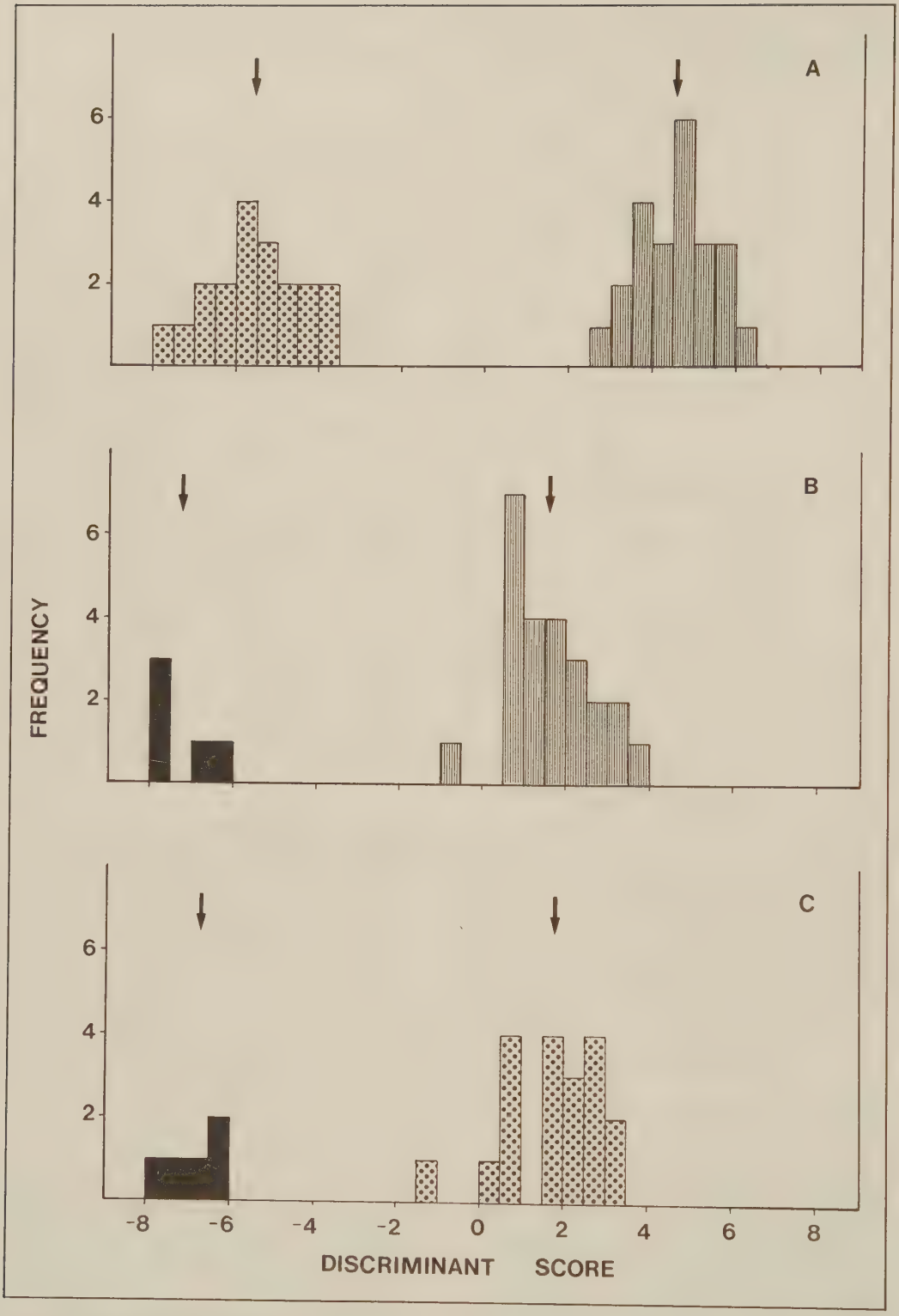


Figure 5—Histograms of discriminant scores from the two-group discriminant function analyses of (A) *A. tropicalis* (stripes) and *A. gazella* (dots), (B) *A. tropicalis* and the interspecific hybrids (solid), and (C) *A. gazella* and the interspecific hybrids. Arrows indicate positions of the mean discriminant scores.

affinity. This provides an accurate means of species identification between specimens of *A. tropicalis* and *A. gazella*, based entirely on cranial characters, and should prove of practical value in the identification of museum material of doubtful origin. At present the discriminant function analyses are limited to adult males of *A. tropicalis*, *A. gazella*, and the interspecific hybrid. The benefits of including other age and sex classes as well as the remaining six arctocephaline species would be great, especially in light of the increasing frequency of vagrant fur seals being recorded (Payne 1979; Shaughnessy and Ross 1980; Kerley 1983c).

From the PCA it is apparent that the hybrid specimens are intermediate in cranial morphology between the two parent species with some specimens tending towards one or the other parent species (e.g., OTU 44). No information is available regarding the parentage of these hybrid individuals. The expected result of a diversity of generations (i.e., F1 and later hybrids, as well as hybrids backbred with the parent species) would be to produce a normal distribution of skull measurements since size is polygenic.

The adult male hybrids can be phenotypically distinguished in the field on the basis of external appearance. This subjective definition of the hybrids is strongly supported by the present multivariate analyses, especially the PCA which has no *a priori* classification. These results support the contention (Condy 1978) that these two species are hybridizing at the Prince Edward Islands. Furthermore, possible hybrids can be identified by means of the discriminant function results with a suite of eight cranial measurements providing maximum separation between *A. tropicalis* and the hybrids (Table 6b, Fig. 5), or nine cranial measurements to separate *A. gazella* and the hybrids (Table 6c, Fig. 5). Caution should be exercised, however, in the classification of putative hybrids which show affinities for the parent species in the discriminant function analysis. Multiple generation hybrids backbred predominantly with one of the parent species would be difficult to distinguish from that species. Further genetic information would be necessary for a decision in such a case.

ACKNOWLEDGMENTS

We are grateful to W. N. Bonner, British Antarctic Survey, for the loan of *A. gazella* material; the staff of the Computer Centre, University of Pretoria, for their help, and M. N. Bester for his advice on aspects of this study. Author G. Kerley received logistical and financial support from the Department of Transport, provided on the advice of the South African Committee for Antarctic Research.

CITATIONS

BONNER, W. N.
1968. The fur seal of South Georgia. Br. Antarct. Surv. Sci. Rep. 56:1-81.
1981. Southern fur seals *Arctocephalus* (Geoffroy Saint-Hilaire and Cuvier, 1826). *In* Ridgway, S. H., and R. J. Harrison (eds.), Handbook of marine mammals, Vol. 1, p. 161-208. Academic Press, London.

CONDY, P. R.
1978. Distribution, abundance and annual cycle of fur seals (*Arctocephalus* spp.) on the Prince Edward Islands. S. Afr. J. Wildl. Res. 8:159-168.

KERLEY, G. I. H.
1983a. Relative population sizes and trends, and hybridization of fur seals *Arctocephalus tropicalis* and *A. gazella* at the Prince Edward Islands, Southern Ocean. S. Afr. J. Zool. 18:388-392.
1983b. Comparison of seasonal haul-out patterns of fur seals *Arctocephalus tropicalis* and *A. gazella* on subantarctic Marion Island. S. Afr. J. Wildl. Res. 13:71-77.
1983c. Record for the Cape fur seal *Arctocephalus pusillus pusillus* from subantarctic Marion Island. S. Afr. J. Zool. 18:139-140.
1984. Relationships between sympatric breeding populations of fur seals (*Arctocephalus* sp.) at the Prince Edward Islands. S. Afr. J. Sci. 80:28-29.
1985. Pup growth in the fur seals *Arctocephalus tropicalis* and *A. gazella* on Marion Island. J. Zool. (Lond.) 205:315-324.

KING, J. E.
1959a. The northern and southern populations of *Arctocephalus gazella*. Mammalia 23:19-40.
1959b. A note on the specific name of the Kerguelen fur seal. Mammalia 23:381.

NEFF, N. A., and L. F. MARCUS.
1980. A survey of multivariate methods for systematics, p. 243. Privately published, New York.

ORR, R. T., J. SCHONEWALD, and K. W. KENYON.
1970. The California sea lion: skull growth and a comparison of two populations. Proc. Calif. Acad. Sci. 37:381-394.

PAYNE, M. R.
1979. Fur seals *Arctocephalus tropicalis* and *A. gazella* crossing the Antarctic Convergence at South Georgia. Mammalia 43:93-98.

REPENNING, C. A., R. S. PETERSON, and C. L. HUBBS.
1971. Contributions to the systematics of the Southern fur seals, with particular reference to the Juan Fernandez and Guadalupe species. Antarct. Res. Ser. 18:1-34.

ROBINSON, T. J., and N. J. DIPPENAAR.
1983. Morphometrics of the South African leporidae I: genus *Pronolagus* Lyon, 1904. Ann. Mus. R. Afr. Cent. Ser. Quarto Zool. 237:43-61.

ROHLF, F. J., J. KISHPAUGH, and D. KIRK.
1974. NT-SYS. Numerical taxonomy system of multivariate statistical programs. State Univ. New York, Stony Brook.

SHAUGHNESSY, P. D., and G. J. B. ROSS.
1980. Records of the subantarctic fur seal (*Arctocephalus tropicalus*) from South Africa with notes on its biology and some observations of captive animals. Ann. S. Afr. Mus. 82:71-89.

SIVERTSEN, E.
1954. A survey of the eared seals (family *Otariidae*) with remarks on the Antarctic seals collected by M/K "Norvegia" in 1928-1929. Skr. nor. Videnskap-Akad. Oslo I Mat.-Naturvidensk. Kl. 36:1-86.

STATISTICAL PACKAGES FOR SOCIAL SCIENCES.
1983. SPSSX users guide. McGraw-Hill, New York.

SWANEPOEL, P., and H. H. GENOWAYS.
1978. Revision of the Antillean bats of the genus *Brachyphylla* (Mammalia: Phyllostomatidae). Bull. Carnegie Mus. Nat. Hist. 12:5-53.

YATES, T. L., H. H. GENOWAYS, and J. K. JONES.
1979. Rabbits (Genus *Sylvilagus*) of Nicaragua. Mammalia 43:113-124.

On Comparing the Population Dynamics of Fur Seals

ANNE E. YORK
National Marine Mammal Laboratory
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE, Bldg. 4
Seattle, Washington 98115

ABSTRACT

A relatively simple age-structured model applicable to most species of fur seals was constructed. Using the model and available data on vital parameters and observed rates of increase or decrease of the various populations of fur seals, I investigated the interrelationships among the vital parameters and their effect on the rate of increase of the population. There are some similarities among the populations: (1) all must have high adult survivorship, i.e., greater than 85% per year; (2) changes in age at first reproduction alone do not greatly affect the rate of increase of the population; and (3) small changes (not statistically detectable without very large sample sizes) in any combination of vital parameters can significantly change the rate of increase of the population. There are also two important dissimilarities: (1) the observed rates of population increase for the southern species (as high as 15-16% per year) are much higher than the maximum rate of increase observed for the Pribilof Island population of northern fur seals (8% per year); and (2) many of the southern populations of fur seals are increasing, whereas most of the populations of northern fur seals have decreased recently or have remained stable. The first suggests that scientists must be circumspect in applying vital parameters estimated for *Callorhinus* to *Arctocephalus*; the second implies that comparisons of population dynamics must take into account the environmental differences which affect the vital parameters. The model also allows one to estimate adult survival if the growth rate and the average age of the breeding females are known.

INTRODUCTION

Models have been developed to describe the dynamics of several fur seal populations and to predict or describe how those populations vary over time. Frisman et al. (1982) modeled the Robben Island population of the northern fur seal, *Callorhinus ursinus*. York and Hartley (1981) modeled the harvested portion of the St. Paul Island population of *C. ursinus* to investigate the relationship of a decline in the fur seal population to a harvest of females. Eberhardt (1981) modeled the dynamics of the Pribilof Island population of northern fur seals during 1950-76 with an emphasis on understanding possible density-dependent effects on juvenile survival. Smith and Polacheck (1981) reexamined the life table of northern fur seals to attempt an understanding of that population's regulatory mechanisms. Chapman (1973) modeled the northern fur seal population to estimate the level of the population necessary to obtain maximum sustainable yield. Shaughnessy and Best (1982) and Shaughnessy and Butterworth (1981) modeled the population dynamics of the South African fur seal, *Arctocephalus pusillus pusillus*, to determine the annual yield of yearlings.

In the present paper, a relatively simple age-structured model was developed that is sufficiently general to be applicable to most species of fur seals. To compare the dynamics of the various populations of fur seals, the available data on some vital parameters for those populations are summarized. The purposes for developing the model were (1) to compare the dynamics of various populations of fur seals for which some vital parameters have been measured and, therefore, (2) to understand, in a general way, how a change in one vital parameter affects the rate of increase or decrease of the population, or how a change in one or two parameters can compensate for changes in other vital parameters and maintain a rate of increase, and (3) to give ranges of values of the unknown vital parameters for those populations for which only some vital parameters are known.

AVAILABLE DATA

Most fur seals breed at very remote locations and are pelagic for some part of their life cycle. Thus, it is difficult, time-consuming, and expensive to measure vital parameters for such species. Table 1 summarizes available information on several vital parameters for females of various populations of fur seals. The vital parameters presented in Table 1 are generalized, that is, less detail is presented than is known for some populations (namely, the populations of northern and Antarctic fur seals) in order to compare parameters among several populations and species.

The rate of increase or decrease of a population is the most frequently reported parameter because it is one of the easiest to measure; it usually arises out of several serial censuses of a component of population. The logarithm of the population is regressed on time, and the exponential of the slope is the estimate of the growth rate of the population.

Adult survivorship is not known for most populations probably because its measurement requires a long-term study of marked cohorts or random samples from a population with a stationary age distribution and known rate of increase. In fact, none of the estimates of adult survival presented in Table 1 were directly measured but were estimated from life tables which were determined from the age composition of a sample. Adult survival has a significant effect on the rate of increase of the population; thus, a small error in the determination of adult survival can invalidate the predictions

Table 1—Estimates of rate of increase or decrease of populations of various stocks of fur seals; estimates of vital parameters with source or method of obtaining the estimate (— indicates no information available).

Production	Annual rate of increase	Number of data points	Adult female survivals (*s*)	Immature female survival (*p*)	Juvenile female survival (*j*)	Age of first reproduction (*a*)	Fecundity (*m*)	Average age of mothers (*T*)
Callorhinus ursinus								
Pribilof Is.	8.0% (1911-24)[2]	9	0.90[9]	0.85[9]	0.14-0.45[8]	4 yr[11]	0.34[9]	10.38[14]
	0.0% (1950-55)[1]	6	—	—	(0-2 yr)	—	—	—
	−6.0% (1955-65)[1]	11						
	0.0% (1965-75)[1]	10						
	−7.8% (1975-81)[1]	5						
	−1.8% (1981-86)[1]	5						
Commander Is.	0.0% (1974-82)[3]	9	—	—	—	3-4 yr[9,12]	0.36[12]	8.23[12]
Robben Is.	−5.8% (1974-82)[3]	9	0.86[10]	0.86[10]	0.2-0.5[10] (0-3 yr)			
Arctocephalus gazella								
South Georgia	13.1% (1958-75)[4]	9	0.92-0.95[4]	—	0.76 (0-1 yr)[4]	3 yr[4]	0.43[4]	7.41[15]
Marion Is.	15.1% (1974-81)[5]	2	—	—	—	—	—	—
A. tropicalis			—	—	—	—	—	—
Gough	15.9% (1955-77)[7]	2	0.95-0.97[22]	—	—	4 yr[20]	0.40[19]	8.4-8.5[19]
Marion Is.	10.5% (1951-74)[6]	2	—	—	—	—	—	—
	15.0% (1974-81)[5]	3	—	—	—	—	—	—
Amsterdam Is.	11.0% (1956-81)[6]	3	—	—	—	—	—	—
	7.8% (1955-69)[21]	2						
	16.5% (1969-81)[6]	2						
A. australis (all stocks)	11.0% (1953-72)[8]	2	—	—	—	4 yr[8]	0.39-0.43[13]	—
A. pusillus pusillus	5.8% (1971-80)[17]	4(?)	—	—	—	4 yr[16]	0.32-0.37[13]	—
A. pusillus doriferus	0.0% (1945-75)[18]	?	—	—	—	4 yr[18]	—	—

[1]Calculated from summary of fur seal pup numbers in U.S. annual reports of fur seal investigations 1963-85.
[2]Lander 1981.
[3]Calculated from data in Soviet annual reports of fur seal investigations 1974-83.
[4]Calculated from the unadjusted pup counts in Payne 1977.
[5]Kerley 1983.
[6]Condy 1978.
[7]Bester 1980.
[8]Vaz-Ferreira 1982.
[9]Lander 1981.
[10]Frisman et al. 1982.
[11]York 1983.
[12]Calculated from data from Japanese pelagic surveys 1958-74.
[13]Calculated from data in Vas Ferreira 1982.
[14]Calculated from information in U.S.-Canadian combined pelagic surveys, 1958-74.
[15]Calculated from data in Payne 1977.
[16]Shaughnessy 1982.
[17]Shaughnessy and Butterworth 1981.
[18]P. Shaughnessy, CSIRO, P. O. Box 225, Dickson ACT, 2602, Australia, pers. commun. April 1984.
[19]M. Bester, Mammal Res. Inst., Univ. Pretoria, Pretoria, S. Afr., pers. commun. April 1984; Bester 1987.
[20]Bester 1987.
[21]Hes and Rouse 1983.
[22]Determined in this paper; please see cautionary note in Results section.

based on a mathematical model of that population (Eberhardt and Siniff 1977; Smith and Polacheck 1981).

Fecundity[1] is reported for several species but the rates are determined in a variety of ways. For *C. ursinus*, fecundity was estimated from pregnancy rates in pelagic samples (sex ratio of fetuses is approximately 1:1). For other species, fecundity was measured on land from animals taken on the breeding islands. It is difficult to determine how representative any fecundity measurement is for fur seals. For example, pelagic measurements of fecundity for *C. ursinus* vary over time (both months and years) and over location (York 1979). The fecundity rates for *C. ursinus* in Table 1 are based on large numbers of seals, but it is not known how representative they are of the population. Measurements of fecundity for *C. ursinus* taken on land also vary. A sample from the rookeries at the height of the breeding season may include 90-99% pregnant or postpartum females, while one taken on haul-out sites can contain as few as 40% pregnant or postpartum females. A sample taken on the breeding area late in the season will have 50-80% pregnant or postpartum (Abegglen and Roppel 1959).

Juvenile survival from birth to age 1 or 2 years is reported for several populations of *C. ursinus* and the Bird Island population

[1]The average number of female offspring born each year to each female older than the average age of first reproduction.

of *A. gazella*. It is known that juvenile survival varies significantly from year to year in *C. ursinus* (Lander 1975, 1979; Frisman et al. 1982); survival estimates in these papers are based on estimates of the utilization rates in the commercial harvests using a method developed by Lander (1975). The juvenile survival estimates for *C. ursinus* in Table 1 are the ranges reported in Lander (1979) and Frisman et al. (1982). Payne (1977) estimates juvenile survival for the Bird Island population of *A. gazella* using a simple population model; thus, that estimate is not for a single cohort but is an average over several cohorts.

The average age of breeding females in the population (generation length) is available for *C. ursinus*, the Bird Island population of *A. gazella*, and the Gough Island population of *A. tropicalis*. Age at first reproduction is available for most populations. The annual survival rate of prereproductive animals older than 2 years is reported only for *C. ursinus*.

METHODS

Description of the model

Suppose we have a population with the following vital parameters:

j, juvenile survival rate from birth to age 2 years;
p, annual survival rate age 2 years to the age at first reproduction (a);
s, the average annual survival rate for animals older than a; and
m, the fecundity rate, the average number of female pups born to each female, for animals ages a to N.

The age at first reproduction is a, and the maximum age of a reproductively active animal is N. Therefore, $N-a+1$ is the maximum number of years a female is reproductively active; jp^{a-2} is the rate of survival from birth to age at first reproduction.

The intrinsic rate of increase of this population (Charlesworth 1980), after the population has acquired a stable age distribution, is ln (λ), where λ is computed in the following way:

$$1 = \sum_{x=a}^{N} (1/\lambda)^{x+1}\, m \cdot j \cdot p^{a-2}\, s^{x-a} \qquad (1)$$

The principal eigenvalue of the Leslie matrix corresponding to this model is λ. Since for our applications the value of the principal eigenvalue is near 1, the annual rate of increase of the population is approximately $\lambda - 1$.

Rewriting equation (1) and using the formula for the sum of a geometric series and combining, the following is obtained:

$$\frac{\lambda^a}{m \cdot j \cdot p^{a-2}} = \sum_{x=a}^{N} (s/\lambda)^{x-a}$$

$$= \frac{1 - (s/\lambda)^{N-a+1}}{1 - (s/\lambda)}$$

Solving for j, the following formula is obtained:

$$j = \frac{\lambda^a}{m \cdot p^{a-2}} \cdot \frac{(1 - s/\lambda)}{1 - (s/\lambda)^{N-a+1}} \qquad (2)$$

The special case in which N is very large and $(s/\lambda)<1$, that is $(s/\lambda)^{N-a+1}$ near 0, was analyzed by Eberhardt and Siniff (1977).

Analysis of the model

To understand how these parameters interact, the survival rate to age 2 (j) was computed using equation (2) for several values of λ, s, and N. It was assumed $p = s$ so that the calculated j is actually a lower bound on the true value of j because, generally, $p < s$. For example, for *C. ursinus*, p is about 0.85 and s is 0.90. The λ is assumed to be between 0.92 and 1.16 (the range of observed λ in various populations of fur seals, Table 1); I assumed that the annual survival rate (p) between ages 2 and a, the age at first reproduction, was the same as the adult survival rate (between 0.75 and 0.99). Two cases for N were examined: In the first, N is assumed to be large and the model is essentially the Eberhardt-Siniff model; in the second, N is assumed to be 25, ($N = 25$ is not an unreasonable maximum age for reproductive *C. ursinus* or *A. gazella*). These λ, a, s, m, and j surfaces appear as five-dimensional figures in Figures 1 and 2.

The average age of breeding females after a stable age distribution is reached (Charlesworth 1980) is:

$$T = \sum_{x=a}^{N} x \cdot s^{x-a}\, (1/\lambda)^x\, m \cdot j \cdot p^{a-2} \qquad (3)$$

Substituting the solution for j from equation (2) into equation (3), one obtains a solution for T in terms of the ratio of s to λ:

$$T = (s/\lambda)^{-a}\, \frac{1 - s/\lambda}{1 - (s/\lambda)^{N-a+1}} \sum_{x=a}^{N} x (s/\lambda)^x \qquad (4)$$

Equation (4) facilitates the investigation of the consistency of the possible range of fecundity, adult survival, and juvenile survival, if an estimate of the average age of breeding females in the population is available.

Payne (1977) gives the age composition of a sample of 198 breeding females from the Bird Island herd of *A. gazella*. The average age of the breeding females was about 7.41 years. From data collected in the eastern North Pacific Ocean by Canadian and U.S. scientists during 1958-74, the average age of the Pribilof breeding population was about 10.38 years. Data collected in the western North Pacific Ocean by Japanese scientists during the same period showed the average age was 8.23 years. By substituting the above estimates of average age of pregnant females (T) into equation (4), one can solve for s/λ if the maximum age of reproductive females (N) and the age at first reproduction (a) are known. Then, if estimates of λ and T are available, the adult survival rate (s), can be approximated.

RESULTS

Using the model and the derived equation for juvenile survival (equation (2)), three-dimensional surfaces were constructed for each combination of λ and age at first reproduction (Figs. 1 and 2). Each three-dimensional surface represents the various combinations of fecundity (m), adult survivals (s), and minimum juvenile survival (j) required to maintain the population increase at approximately $\lambda-1$ with the given age at first reproduction (a). Thus, Figures 1

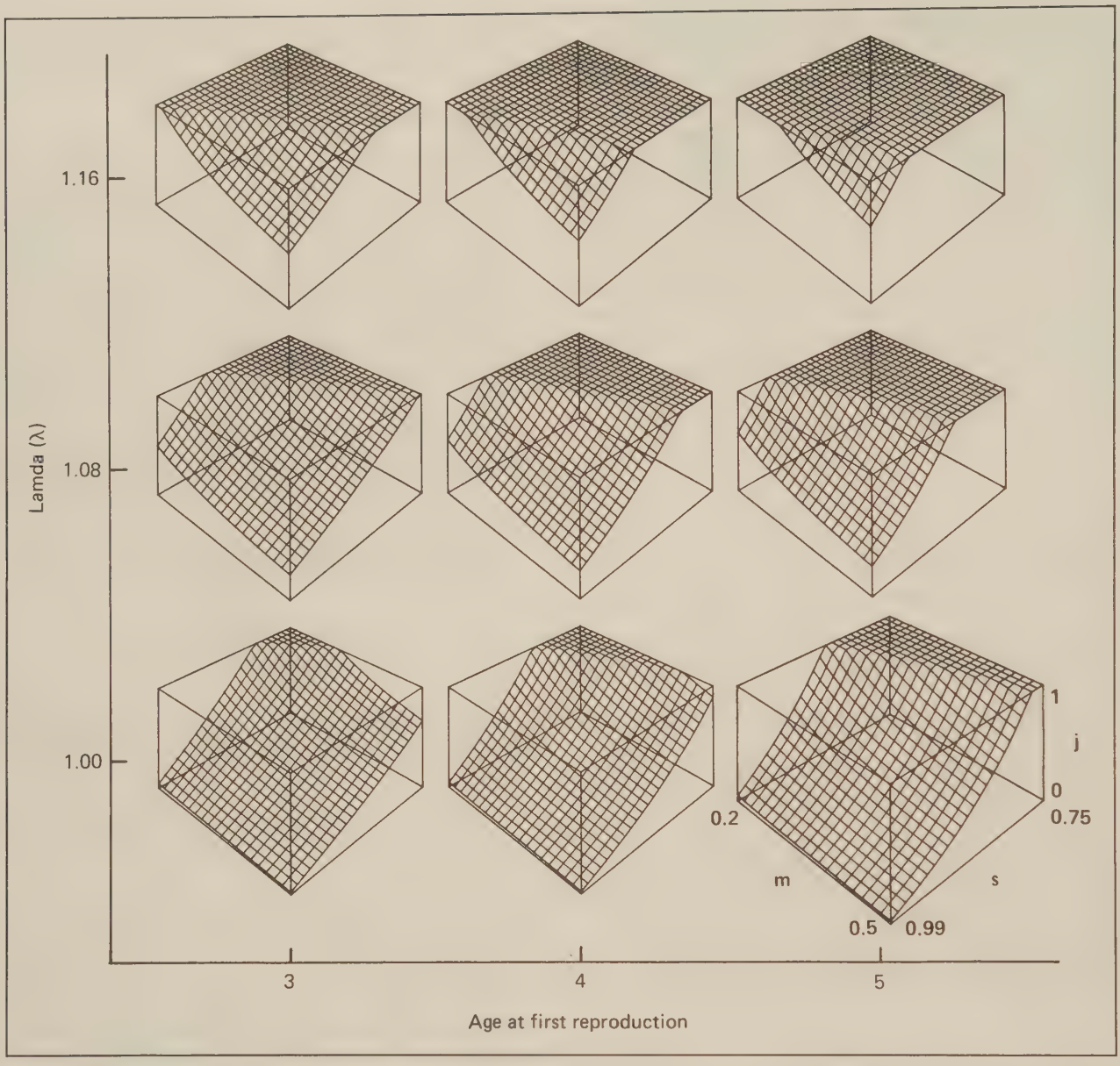


Figure 1—Combinations of fecundity ($0.2<m<0.5$), adult survival ($0.75<s<0.99$), and juvenile survival ($0<j<1$) required to maintain an intrinsic rate of increase of approximately $1-\lambda$ for the given age at first reproduction. (It is assumed that $s<\lambda$ and that there is no maximum largest age (N)).

and 2 indicate how the five parameters interact and how changes in various other vital parameters affect juvenile survival; in particular, the figures show the manner in which the surfaces change with increasing λ or a. In Figure 2, the maximum age for reproductive females is 25 years, but in Figure 1 there is no bound except, of course, the practical bound placed on the maximum age by the value of adult survival. Thus, Figure 1 is a representation of the Eberhardt-Siniff model (1977) and Figure 2 the somewhat more complicated model. The juvenile survival surfaces in Figure 1 are slightly lower than those for the corresponding values of age at first reproduction and λ in Figure 2 because the total number of reproductively active years is larger.

The particular values of λ were chosen because they are near those observed for the various populations of fur seals (Table 1). The values of age at first reproduction (a) were chosen to be 3, 4, and 5 because this is the range of age at first reproduction observed for various species of fur seals (e.g., *C. ursinus*, *A. gazella*, *A. p. pusillus*, *A. p. doriferus*, and *A. tropicalis*; no data were available for *A. philippii*, *A. townsendi*, *A. australis*, or *A. galopagoensis* which may have higher ages at first reproduction). In Figures 1 and 2, fecundity ranges from 0.2 to 0.5 and adult survival from 0.75 to 0.99. These ranges were chosen because the empirical data suggest these are reasonable limits. Furthermore, the calculations using equation (2) indicate that for most situations, adult survivorship must be quite large to simply stabilize the population (i.e., if $\lambda=1$) and even higher if the population is growing (i.e., if $\lambda>1$).

For some combinations of fecundity and juvenile survival, the value of juvenile survival required to maintain the indicated rate of increase with the indicated age at first reproduction is larger than 1. These combinations are called "inadmissible" combinations because such combinations of λ, a, s, and m give rise to solutions for juvenile survival (equation (2)) which are greater than 1. In

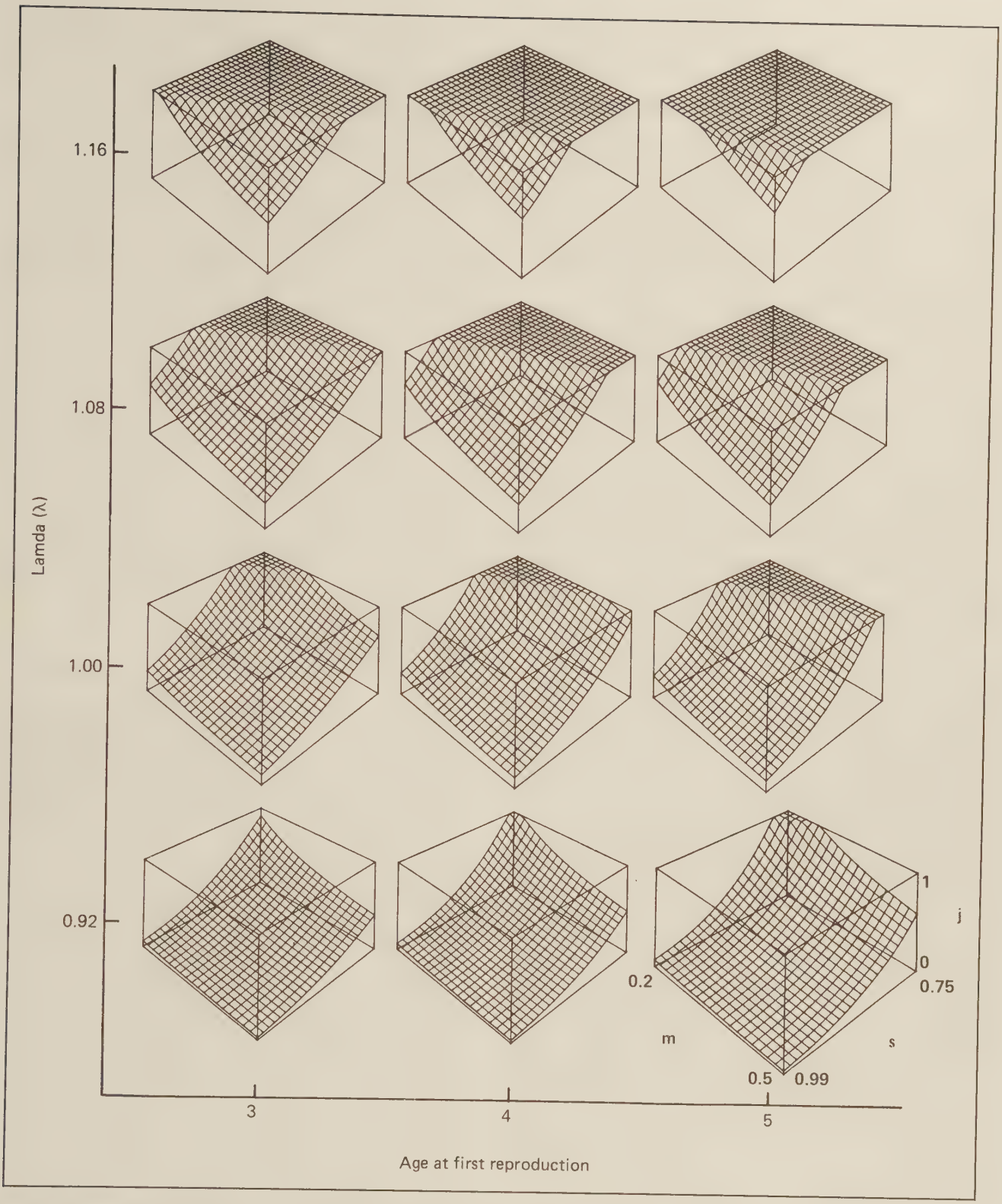


Figure 2—Combinations of fecundity ($0.2<m<0.5$), adult survival ($0.75<s<0.99$), and juvenile survival ($0<j<1$) required to maintain a population increase of approximately $1-\lambda$, age at first reproduction (a), and (N), the maximum age of breeding females 25 yr.

Figures 1 and 2, these situations are apparent for those combinations in which the juvenile survival surface is flat at the top of the prism.

A proper analysis of the effects of small changes in one of the variables (λ, a, m, or s) on the resulting j (from equation (2)) requires computation of the partial derivative of j with respect to the variables in question and an analysis of the behavior of that derivative while holding the other variables constant. Instead of obscuring the underlying phenomena with complicated algebraic manipulations, I have chosen to describe these effects in somewhat general ways and to specify them for some of the populations whose vital parameters are reported in Table 1.

Both Figures 1 and 2 show that age at first reproduction does not have a strong effect on juvenile survival at low levels of λ, but that the effect is somewhat stronger for larger values of λ. This is a consequence of the assumption of equal survival rate for all animals older than age a; when λ is large and the population is increasing, a delay of 1 year in beginning reproduction reduces the number of pups born to a greater degree than a 1-year delay for an older age at first reproduction (Fowler et al. 1980). Therefore, if λ remains the same, and the population continues to grow at the same rate, juvenile survival must correspondingly increase (assuming m and s do not change). This effect is seen in Figure 2: the percentage of inadmissible combinations of fecundity and adult survival grows from 6% at age 3 to 24.1% at age 5 for $\lambda=1.0$ (a 9% change for each yearly increase in age at first reproduction), whereas that same percentage grows from 71% at age 3 to 93% at age 5 at $\lambda=1.16$ (an 11% increase for each yearly increase in age at first reproduction). In addition, the lowest value of j on the surface (corresponding to adult survival of 0.99 and fecundity 0.5) requires a juvenile survival of 0.02 (for both $a=3$ and $a=5$) at $\lambda=1$, whereas, when $\lambda=1.16$, the values are 0.46 for $a=3$ and 0.63 for $a=5$. A comparison of Figures 1 and 2 indicates that the effect of age at first reproduction on juvenile survival is somewhat stronger in Figure 2, wherein the maximum reproductive age is 25.

The effect of fecundity on juvenile survival is negatively proportional to juvenile survival and inversely proportional to fecundity. (This follows from the calculation of the partial derivative of j with respect to m, $\partial j/\partial m = -j/m$). Thus, the effect of a small change in fecundity is greater for smaller values of fecundity and larger values of juvenile survival. For example, in the neighborhood of the average observed fecundity and survival rates for *C. ursinus* females ($m=0.34$, $s=0.90$), a decrease of 0.0l in absolute fecundity (about a 3.2% decrease) would require a compensatory increase of about 0.01 in absolute juvenile survival (approximately 3.1% increase) to maintain the same level of population increase with no increase in any other vital parameter. In the neighborhood of the approximate fecundity and juvenile survival rates for *A. gazella*, a decrease of 0.01 in fecundity (about a 3% decrease) would require a compensatory increase of about 0.06 in absolute juvenile (or about an 8% increase) to maintain the same level of increase of the population with no other compensatory change in vital parameters.

The effect of adult survival on the computed juvenile survival is substantial but it is difficult to separate it from the values of other vital parameters and to describe in a simple way. In the neighborhood of observed values of adult survival for *C. ursinus* (eastern Pacific population), a decrease of 0.01 in adult survival (about a 1.1% decrease) requires a compensatory increase of 0.04 or 10.5% in juvenile survival or an increase of about 0.03 or 10% in fecundity to maintain λ with same age at first reproduction. For the Bird Island population of *A. gazella*, a decrease of 0.01 in adult survival (slightly larger than 1% decrease) requires a compensatory increase of 0.04 or 5.2% in juvenile survival or an increase of 0.02 or 4.6% in fecundity to maintain λ at 1.16. In both cases, the compensation could take place with smaller increases in both juvenile survival and fecundity.

Figure 3 relates information on the average age of breeding females in the population to s/λ (equation (4)) for three values of age at first reproduction (3, 4, and 5) and two values of maximum age of breeding females ($N=20$ and $N=25$). The values of $N=20$ and $N=25$ were chosen because they appear to be approximate bounds on the maximum age of reproductive females for the species considered. There is no difference between the curves for each value of age at first reproduction for $s/\lambda < 0.72$. For $s/\lambda \geq 0.72$, the average age of reproductive females increases more rapidly as the maximum age of reproductive females (N) is allowed to increase. Values of s/λ were estimated for each population for which estimates of T were available. These estimates are presented in Table 2 with values of N and age at first reproduction (a) that were used for the calculations. The estimate of s/λ coupled with an estimate of λ allows us to approximate adult survival, s. These estimates of s also appear in Table 2. Calculated estimates of s in Table 2 are very near those values reported previously in Table 1. This method allows us to make a preliminary estimate of adult survival for *A. tropicalis* at Gough Island of approximately 0.95-0.97 based on a mean age of 8.45 yr from an aged sample of pregnant females (M. Bester, Univ. Pretoria, pers. commun.).

DISCUSSION

This paper develops a general age-structured population model applicable to a number of species of fur seals. The model is not intended to mimic the population dynamics of any particular stock but rather to be a tool for examining the interrelationship of the vital parameters and understanding in a general way the magnitude of compensatory effects of small and sometimes undetectable (given available sample sizes) changes in some vital parameter. Thus, conclusions about the dynamics of a particular population must not be taken literally since for those stocks whose population dynamics are better understood, the model simplifies reality a great deal. However, the model is useful for cross-population comparisons of a general nature, and this is its principle use in the present paper. The analysis of the contents of Figures 1 and 2 emphasizes the danger of applying estimates of vital parameters from one population to another. When the value of a vital parameter is not known, and a value is assumed because it is known for a similar species, that assumption may force unlikely combinations of vital parameters or warp our understanding of the relationship among the vital parameters for the species to which the assumed values are applied.

The concept developed in equations (3) and (4) illustrated in Figure 3 is a useful tool for limiting the predicted range of vital parameters; estimates of adult survival derived from equation (4) and presented in Table 2 closely approximate those in Table 1 for the western Pacific population of *C. ursinus* and the Bird Island population of *A. gazella*. The estimate of adult survival for the Pribilof population of *C. ursinus* in Table 2 is nearly identical to that of the western Pacific population. The discrepancy between the adult survival estimates in Tables 1 and 2 is due to mortality from the commercial harvest of females during 1956-68. Life tables developed by Lander (1981) assumed that the population was stable in this period in order to estimate natural mortality rather than total mortality. If the assumption of stability is made, and λ is assumed

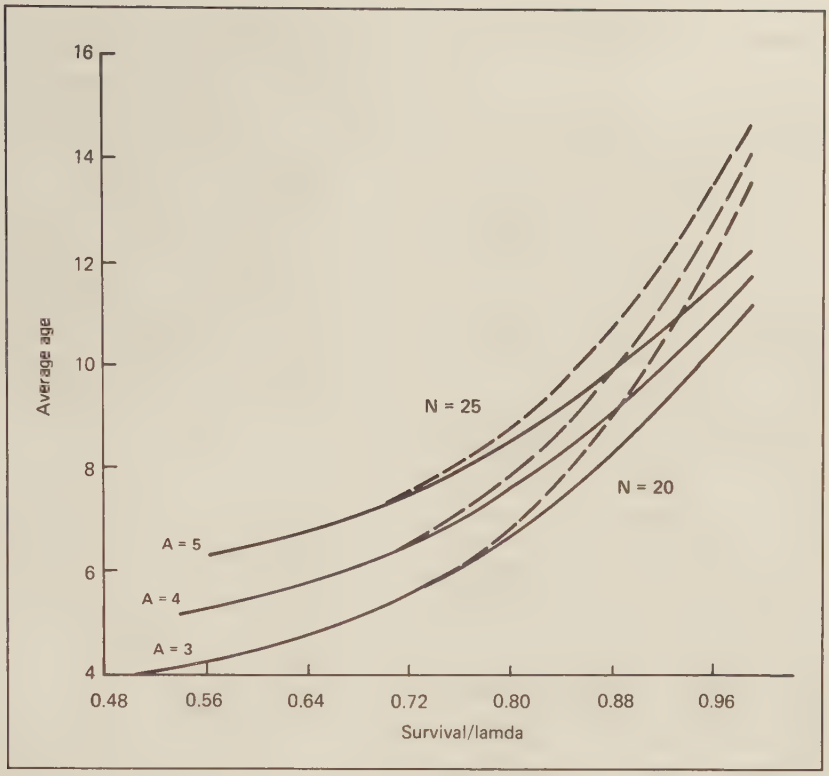


Figure 3—Average age of reproducing females as a function of the ratio of adult survival to lamda (the exponential of the rate of increase of the population) for age at first reproduction (*a*) 3, 4, and 5, and the maximum age of reproducing females (*N*) 20 and 25.

Table 2— Average age of breeding females (*T*), estimated ratio of adult survival to λ (the exponential of the rate of increase of the population), (λ/*s*), the estimate of λ during the period that the average age of breeding females was collected, and estimated adult survival (*s*).

Population	*T*	*s*/λ	*N*	*a*	λ	*s*
C. ursinus, Pribilof	10.38	0.8938	25[1]	4	0.95	0.849
					1.00	0.894
C. ursinus, W. Pacific	8.23	0.8604	23[1]	3	1.00	0.860
A. gazella, Bird Is.	7.41	0.8282	23[2]	3	1.13	0.936
A. australis, Gough Is.	8.43	0.8439-8489	20	4	1.15	0.970-0.976
	−8.5	0.8305-8349	23			0.955-0.96
		0.8255-8296	25			0.949-0.954

[1]Determined from the age composition of pelagic samples, 1958-74.
[2]Determined from the age composition of samples reported in Payne (1977)
[3]M. Bester, Univ. Pretoria, pers. commun.

to be 1, then the calculated survival in Table 2 would equal the value in Table 1. The estimates of adult survival of the Gough Island population of *A. tropicalis* range between 0.95 and 0.98 and are near but somewhat larger than the estimates of adult survival for *A. gazella*. If the estimate of the mean age is biased, then the corresponding estimate of *s* will be biased in the same direction. The estimate of average age of reproducing females for *A. tropicalis* reported in Table 1 could well be upwardly biased because it was based on animals found dead on the rookeries (M. Bester, Univ. Pretoria, pers. commun.).

The technique for estimating adult survival from equation (4) is a variation on the Chapman-Robson estimate of survival (Chapman and Robson 1960); the variability and bias of this estimate must be studied before the technique can be generally applied. Furthermore, although the estimate appears to be valid even if the assumption of equal adult survivorship is violated, formal studies of the statistical properties of the estimate must be conducted before the results are strongly believed.

ACKNOWLEDGMENTS

I wish to thank those who attended the 1984 Fur Seal Symposium in Cambridge for generously sharing unpublished data on the various species of fur seals. Howard Braham, Jeffrey Breiwick, Charles Fowler, Harvey Friedman, and A. E. Kuzin reviewed the manuscript and provided valuable suggestions for its improvement. M. Bester was most helpful in providing references and sorting out many details in Table 1. Roger Pearson helped clarify the presentation of some of the obtuse mathematical ideas.

CITATIONS

ABEGGLEN, C. E., and A. Y. ROPPEL.
1959. Fertility in the northern fur seal, 1956-1957. J. Wildl. Manage. 23:75-81.

BESTER, M. N.
1980. Population increase in the Amsterdam Island fur seal *Arctocephalus tropicalis* at Gough Island. S. Afr. J. Zool. 15:229-234.
1987. Subantarctic fur seal, *Arctocephalus tropicalis*, at Gough Island (Tristan Da Cunna Group). *In* Croxall, J. P., and R. L. Gentry (eds.), Status, biology, and ecology of fur seals, p. 57-60. U.S. Dep. Commer., NOAA Tech. Rep. 51.

CHAPMAN, D. G.
1973. Spawner-recruit models and estimation of the level of maximum sustainable catch. Rapp. P.-V. Reun. Cons. int. Explor. Mer 164:325-332.

CHAPMAN, D. G., and D. S. ROBSON.
1960. The analysis of a catch curve. Biometrics 16:354-368.

CHARLESWORTH, B.
1980. Evolution in age-structured populations. Cambridge Univ. Press, Cambridge, U.K., 300 p.

CONDY, P. R.
1978. Distribution, abundance, and annual cycle of fur seals (*Arctocephalis* spp.) on the Prince Edward Islands. S. Afr. J. Wildl. Res. 8:159-168.

EBERHARDT, L. L.
1981. Population dynamics of the Pribilof fur seals. *In* Fowler, C. W., and T. D. Smith (eds.), Dynamics of large mammal populations, p. 197-200. John Wiley and Sons, N.Y.

EBERHARDT, L. L., and D. B. SINIFF.
1977. Population dynamics and marine mammal management policies. J. Fish. Res. Board Can. 34:183-190.

FOWLER, C. W., W. T. BUNDERSON, M. B. CHERRY, R. J. RYEL, and B. B. STEELE.
1980. Comparative population dynamics of large mammals: a search for management criteria. Mar. Mammal Comm., Wash., D.C., 158 p. (Avail. as PB80-178627 from U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va.

FRISMAN, E. Ya., E. I. SKALETSKAYA, and A. E. KUZIN.
1982. A mathematical model of the population dynamics of a local northern fur-seal herd. Ecol. Model. 16:151-172.

HES, A. D., and G. P. ROUSE.
1983. Population increase in the sub-Antarctic fur seal *Arctocephalus tropicalis* at Amsterdam Island. S. Afr. J. Antarct. Res. 13:29-34.

KERLEY, G. I. H.
1983. Relative population sizes and trends, and hybridization of fur seals, *Arctocephalus tropicalis* and *A. gazella* at the Prince Edward Islands, Southern Ocean. S. Afr. J. Zool. 18:388-392.

LANDER, R. H.
1975. Method of determining natural mortality in the northern fur seal (*Callorhinus ursinus*) from known pups and kill by age and sex. J. Fish. Res. Board Can. 32:2447-2452.
1979. Role of land and ocean mortality in yield of Alaska fur seals. Fish Bull., U.S. 77:311-314.
1981. A life table and biomass estimate for Alaskan fur seals. Fish. Res. 1:55-70.

PAYNE, M. R.
1977. Growth of a fur seal population. Philos. Trans. R. Soc. Lond., B Biol. Sci. 279(963):67-80.

SHAUGHNESSY, P. D.
1982. The status of seals in South Africa and Namibia. *In* Mammals in the seas, p. 361-382. FAO Fish. Ser. 5, Vol. 4.

SHAUGHNESSY, P. D., and P. B. BEST.
1982. A discrete population model for the South African fur seal, *Arctocephalus pusillus pusillus*. *In* Mammals in the seas, p. 163-176. FAO Fish. Ser. 5, Vol. 4.

SHAUGHNESSY, P. D., and D. S. BUTTERWORTH.
1981. Historical trends in the population size of the cape fur seal (*Arctocephalus pusillus*). *In* Chapman, J. A., and D. Pursley (eds.), Proc., Worldwide Furbearer Conference, vol. 2, p. 1305-1327. Worldwide Furbearer Conf., Inc., Frostburg, Md.

SMITH, T. and T. POLACHECK.
1981. Reexamination of the lifetable for northern fur seals with implications about population regulatory mechanisms. *In* Fowler, C. W., and T. D. Smith (eds.), Dynamics of large mammal populations, p. 99-120. John Wiley and Sons, N.Y.

VAZ-FERREIRA, R.
1982. *Arctocephalus australis* (Zimmermann): South American fur seal. *In* Mammals in the seas, p. 497-510. FAO Fish. Ser. 5, Vol. 4.

YORK, A. E.
1979. Analysis of pregnancy rates of female fur seals in the combined United States-Canadian pelagic collections, 1950-1974. *In* Kajimura, H., R. H. Lander, M. A. Perez, A. E. York, and M. A. Bigg, Preliminary analysis of pelagic fur seal data collected by the United States and Canada during 1958-74, p. 50-122. Manuscr. rep. submitted to 22nd Annu. Meet., Stand. Sci. Committee, N. Pac. Fur Seal Comm., Wash., D.C. Aval. Natl. Mar. Mamm. Lab., Seattle, WA 98115.
1983. Average age at first reproduction of the northern fur seal (*Callorhinus ursinus*). Can. J. Fish. Aquat. Sci. 40:121-127.

YORK, A. E., and J. R. HARTLEY.
1981. Pup production following harvest of female northern fur seals. Can. J. Fish. Aquat. Sci. 38:84-90.

Modeling the Population Dynamics of the South African Fur Seal *Arctocephalus pusillus pusillus*

DOUGLAS S. BUTTERWORTH
Department of Applied Mathematics
University of Cape Town
Rondebosch 7700
South Africa

JEREMY H. M. DAVID
Sea Fisheries Institute
Marine Mammal Laboratory
P.O. Box 251
Cape Town 5000
South Africa

LESLEY H. McQUAID[1]
Department of Applied Mathematics
University of Cape Town
Rondebosch 7700
South Africa

SIBUSISO S. XULU[2]
Department of Applied Mathematics
University of Cape Town
Rondebosch 7700
South Africa

ABSTRACT

Aerial survey and tag-recapture assessments of fur seal pup population numbers are considered at the 23 breeding colonies around the southeastern and western coasts of southern Africa during the period 1971-83. Exponential growth curves are fitted for each colony assuming a constant relative bias between the various assessment methods used. The pup population for all colonies combined is estimated to have grown at an average annual rate of 3.9% (SE 1.1%). The population is now dominated by four major mainland colonies which contribute 78% to the 1983 total pup population estimate of 310,000. Mainland colonies have increased over the period considered at an average annual rate of 7.5% (SE 1.5%), while island colonies have declined at 3.5% (SE 0.9%) per annum. Estimation of change in the growth rate suggests that this rate has increased over the period, though not significantly ($P = 0.07$).

No direct assessments are available for adult and juvenile survival rates for the South African fur seal *Arctocephalus pusillus pusillus*, but limitations can be placed on possible ranges of values. An approach is suggested which imposes the constraint of a population dynamics model for adult females upon these ranges, estimates of total pup population size and growth rate, and knowledge of the average annual harvest of pups from 1971 to 1983. This provides refined probability distributions for various demographic parameters; the annual average pup harvesting rate is estimated to have been 37% (SE 5%), and the annual adult female survival rate 0.92 (SE 0.02%). An example is given of how the approach can be extended to provide estimates for sustainable yields. In order to improve the precision of estimates for the total population and to detect possible density-dependent effects, priority should be given to further assessments of the major mainland colonies, particularly those at Wolf and Atlas Bays.

[1]Current address: Department of Zoology, Rhodes University, P.O. Box 94, Grahamstown 6140, South Africa.

[2]Current address: Department of Applied Mathematics, University of Zululand, Private Bag X1001, Kwa-dlangezwa 3886, South Africa.

INTRODUCTION

South African fur seals, *Arctocephalus pusillus pusillus*, are distributed around the southeastern and western coasts of southern Africa, from Algoa Bay (lat. 34°S, long. 26°E) in the southeast to Cape Frio (lat. 18°30′S, long. 12°E) in the northwest. Twenty-three discrete breeding colonies occur along this 3,000-km coastline, of which 17 colonies are situated on small rocky islands and 6 (including the 4 largest) are on the mainland (Fig. 1). Regular migratory movements do not occur in this species (Rand 1956). Pupping and mating take place during the summer months of November and December. Females with pups return regularly to the rookery throughout the year, since most pups are weaned only shortly before the birth of the next pup. Large bulls are mostly absent except during the breeding season.

Fur seals were harvested intensively and indiscriminately by Dutch, French, and British sealers from the early 17th century, and by the time the first legal protection was introduced in 1893 over 20 island colonies had been destroyed. As a result of this uncontrolled exploitation for which there are no comprehensive catch statistics, the seal population was reduced to very low levels by the beginning of the 20th century (Shaughnessy 1984). Since then, under more enlightened management the population has grown rapidly, especially over the past 40 years. This growth has continued despite continued harvesting almost every year. The total known harvest of pups and bulls from 1900 to 1983 was over 2.5 million, and the average annual harvest was about 73,000 pups from 1971 to 1983.

The provision of appropriate management advice for the South African fur seal colonies is critically dependent on quantitative assessment of the population's demographic parameters. Regular aerial surveys and tag-recapture exercises have been carried out at the various breeding colonies since 1971 to determine pup population sizes. In this paper, these results are analyzed to provide growth rate and pup population size estimates, with associated standard errors, for each colony and for the population as a whole. Further, these last estimates, together with the known pup harvest rate, are utilized in a model of the population dynamics to provide information on parameters about which little is known, such as adult and juvenile survival rates. Throughout this paper, the term "significantly different" refers to a difference statistically significant at the 5% level.

ESTIMATION OF COLONY SIZES AND INCREASE/DECREASE RATES

Methods used to obtain basic data

Pup population numbers at the various colonies have been assessed at various times using two methods: aerial photography and tag-recapture.

Aerial photography—Serial overlapping black-and-white photographs are taken from a height of about 130 m at selected colonies each year and at all colonies at 3-4 year intervals. The numbers of black pups are counted on large format glossy prints, 50×40 cm. The photographs are taken between 17 and 22 December each year when the birth season is complete and peak pup numbers are expected. At this time the pups are on average about 3 weeks old. Aerial photography results have been grouped into two categories: AM censuses, carried out for mainland colonies, and AI censuses, carried out for island colonies. Mainland and island colonies have

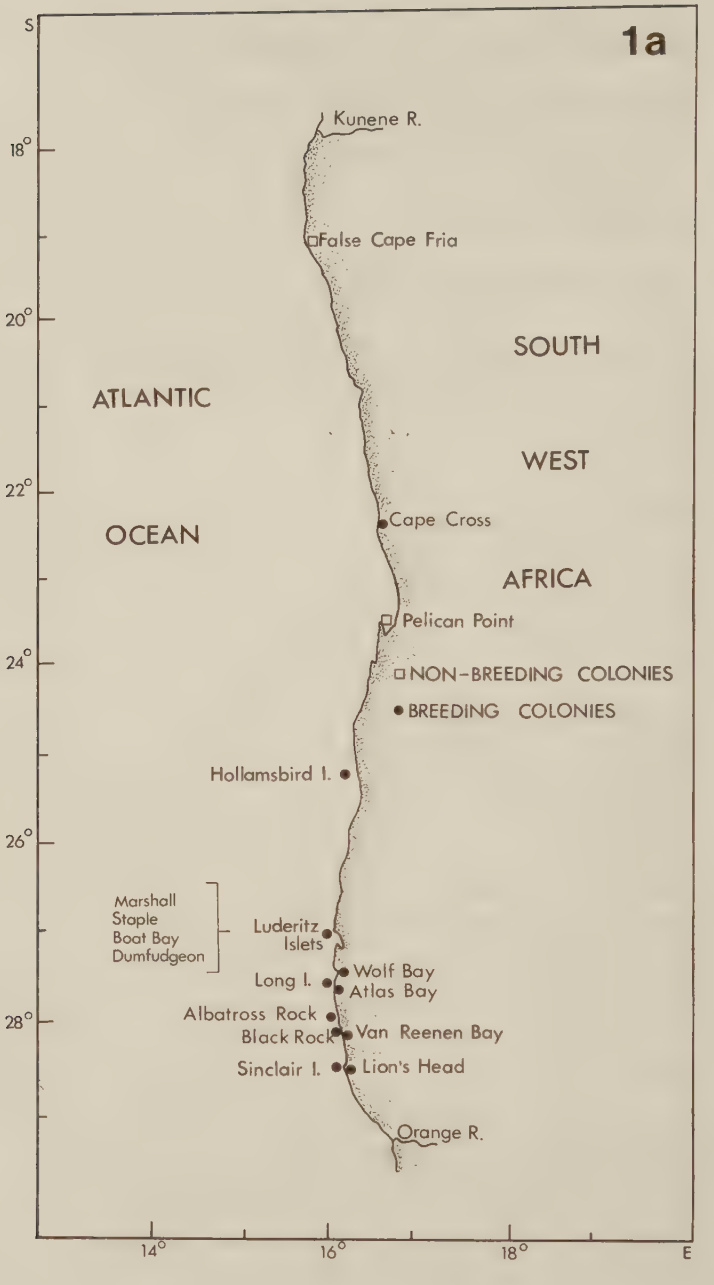


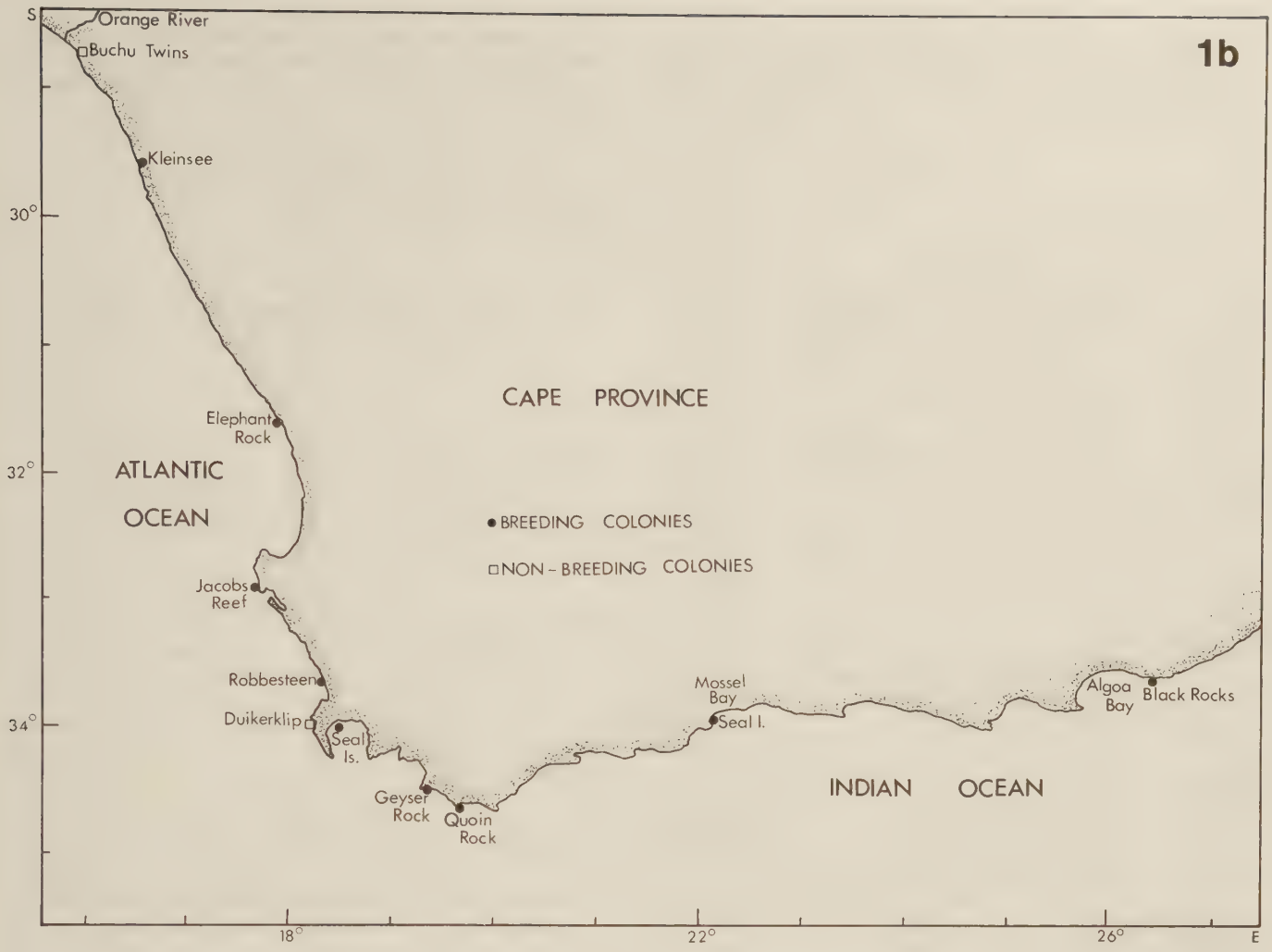
Figure 1—Positions of present breeding and nonbreeding South African fur seal colonies north (a) and south (b, opposite page) of the Orange River.

been distinguished because the mainland colonies have less rocky cover. Counts may therefore be affected to different extents for the two groups by factors such as shadow, and hence the assessments may be biased to differing degrees.

Results of aerial surveys (Shaughnessy In press a,b; Sea Fish. Res. Inst. unpubl. data) over the period 1971-83 are listed in Table 1 (except some 1983 surveys for which the photographs are not yet processed); no standard error estimates are available for these assessments. To avoid confusion concerning years, all new pups are assumed "born" on 1 January and allocated to the corresponding year, even though the median birth date is in the preceding December. Hence an aerial census in, say, December 1976 has been denoted as 1977 in Table 1.

Tag-recapture—Tagging of pups is carried out in mid-January at selected colonies when the pups average about 6 weeks old. Three different assessments of population sizes are obtained, based on different recaptures at later times. The first such assessment is termed *TR*. These data are obtained approximately 1 week after tagging. Groups of pups are surrounded, and the total numbers of pups and tagged pups in each group are counted. Later in the year (between July and September), harvesting of the pups takes place. Data on the proportion of tagged animals harvested provide another tag-recapture assessment termed *H* (for harvest).

Provided there is no differential mortality between tagged and untagged pups over the period from tagging to harvest, the *H* and the *TR* assessments both provide values for the number of pups present at the time tagging took place. However, the proportion of females among tagged pups harvested is consistently less than among untagged harvested pups (Shaughnessy In press b) because



tagged female pups suffer greater mortality than tagged males. (This is not unexpected, as male pups are heavier and more robust than females.) For this reason, *H* assessments have been separated on the basis of sex to provide *HM* and *HF* values. Pups are sexed when tagged, and it is also possible to sex those tagged pups harvested (unlike the situation for the recaptures in the *TR* method). Thus the proportions of tagged male and tagged female pups recovered at harvest, together with the total number of pups harvested, provide independent estimates of the total pup population (*HM* and *HF*, respectively).

Results from these methods (Shaughnessy In press a; Sea Fish. Res. Inst. unpubl. data) over the period 1971-83 are also shown in Table 1. Standard error estimates are indicated as well; they have been obtained through consideration of the results of successive recapture samples and correspond to coefficients of variation averaging 14%.

Only six assessments have been omitted from the list of 132 in Table 1. For one Cape Cross harvest, data were not differentiated by sex. Three Wolf Bay and one Atlas Bay aerial surveys and one Wolf Bay *TR* assessment, all carried out in the early 1970s, were excluded as they gave results considerably lower than harvests taken from those colonies later in the corresponding year. Shaughnessy (In press a) concludes that those particular aerial surveys failed to photograph the complete colonies. No other marked discrepancies of this nature are evident in the data. Further details of the assessment techniques are given in Shaughnessy (In press a,b).

Calculation procedures

Two sets of assumptions have been made to estimate pup population sizes and trends:

1) Each assessment method (m: $m = 1 \ldots M$) provides values biased by a constant relative factor B_m. This factor is independent of the colony under consideration, the year in which the assessment was made, and the size of the population of that colony. There are five such factors, corresponding to the methods *AM*, *AI*, *TR*, *HM* and *HF*. (The justification for this assumption is discussed in Appendix A1.)

2) Each colony (c: $c = 1 \ldots C$) is increasing (or decreasing) exponentially at a rate r_c per annum, which is taken to be independent of time and to remain constant as the size of the colony changes.

An isolated colony with unchanging birth and survival rates would indeed manifest exponential growth in accordance with the latter assumption. This, however, was not the principal motivation for such choice. Over the 13-year period under consideration (1971-83), assessments are available for an average of only 3.4 of those years for any one particular colony; only for 3 of the 23 colonies are assessments available for as many as 5 years. In such circumstances it would be unreasonable to hope to obtain more than some estimate of the average population trend for each colony over the period, and the exponential form is the simplest convenient manner of representing such trend. Density-dependent and immigration effects could well produce population trajectories deviating from the

Table 1—Assessments of fur seal pup population size made at various South African fur seal colonies, 1971-83, using aerial census and tag-recapture methods. Next to the colony name the designations M, I, S, and U refer to mainland, island, sealed, and unsealed, respectively. Colonies are listed in geographical order within each designation, commencing with the northernmost and then moving south and eastward. The right column shows the expected result using the model of equation (2); the parenthesized figure is the percent deviation of the observed assessment from that of the model.

Colony	Observed assessment				Model population size
	Year	Method	Population size	Standard error (C.V.)	
Cape Cross MS	1972	*AM*	17,826		19,463 (−8.41)
	1977	*AM*	22,134		17,511 (26.40)
	1980	*AM*	16,327		16,436 (−0.66)
	1980	*TR*	18,260	2,128(0.117)	21,077(−13.37)
	1980	*HF*	36,949	5,496(0.149)	30,993 (19.22)
	1980	*HM*	20,036	2,089(0.104)	23,798(−15.81)
Wolf Bay MS	1974	*HF*	27,943	6,108(0.219)	28,072 (−0.46)
	1974	*HM*	21,655	4,269(0.197)	21,555 (0.46)
	1979	*AM*	17,961		21,803(−17.62)
	1979	*TR*	30,278	3,401(0.112)	27,961 (8.29)
	1979	*HF*	49,389	6,085(0.123)	41,115 (20.12)
	1979	*HM*	29,462	2,759(0.094)	31,570 (−6.68)
Atlas Bay MS	1974	*AM*	23,295		29,012(−19.70)
	1974	*TR*	37,931		37,205 (1.95)
	1974	*HF*	63,589	5,286(0.083)	54,708 (16.23)
	1974	*HM*	52,286	3,936(0.075)	42,008 (24.47)
	1977	*AM*	25,278		38,584(−34.49)
	1979	*AM*	56,037		46,662 (20.09)
	1979	*TR*	54,151	5,836(0.108)	59,840 (−9.51)
	1979	*HF*	94,501	8,364(0.089)	87,992 (7.40)
	1979	*HM*	74,609	4,738(0.064)	67,565 (10.43)
Kleinsee MS	1972	*AM*	30,429		25,116 (21.15)
	1973	*AM*	27,776		27,718 (0.21)
	1973	*TR*	30,006	4,259(0.142)	35,546(−15.59)
	1973	*HF*	46,332	5,593(0.121)	52,270(−11.36)
	1973	*HM*	37,719	5,042(0.134)	40,136(− 6.02)
	1977	*AM*	52,870		41,120 (28.57)
	1980	*AM*	59,165		55,274 (7.04)
	1981	*TR*	62,535	7,800(0.125)	78,230(−20.06)
	1981	*HM*	78,649		88,329(−10.96)
	1981	*HF*	137,555	20,310(0.148)	115,034 (19.58)
Van Reenen Bay	1972	*AM*	3,241		3,241 (0.00)
MU	1980	*AM*	3,591		3,591 (0.00)
Lions Head MU	1972	*AM*	2,767		2,767 (0.00)
	1977	*AM*	3,265		3,265 (0.00)
Marshall Reef IS	1972	*AI*	755		781 (−3.31)
	1977	*AI*	388		317 (22.40)
	1978	*AI*	259		265 (−2.15)
	1978	*TR*	248	14(0.056)	287(−13.65)
Staple Rock IS	1972	*AI*	2,908		3,199 (−9.09)
	1977	*AI*	2,128		2,103 (1.18)
	1978	*AI*	2,485		1,934 (28.49)
	1978	*TR*	2,043	260(0.127)	2,098 (−2.64)
	1978	*HM*	2,376	469(0.197)	2,369 (0.28)
	1978	*HF*	3,538	889(0.251)	3,086 (14.66)
	1980	*AI*	1,236		1,635(−24.42)
Boat Bay Rock IS	1972	*AI*	1,689		1,851 (−8.74)
	1977	*AI*	1,121		954 (17.55)
	1978	*AI*	984		835 (17.81)
	1978	*TR*	870	143(0.164)	906 (−4.00)
	1980	*AI*	528		641(−17.59)
Dumfudgeon Rock	1972	*AI*	2,873		2,554 (12.50)
IS	1977	*AI*	791		866 (−8.67)
	1978	*AI*	921		698 (32.01)
	1978	*TR*	661	66(0.100)	757(−12.68)
	1978	*HM*	872	346(0.397)	855 (2.02)
	1978	*HF*	677	268(0.396)	1,113(−39.18)
	1980	*AI*	616		453 (36.07)
Long Islands IS	1972	*AI*	12,219		13,097 (−6.70)
	1977	*AI*	10,124		13,791(−26.59)
	1977	*TR*	15,155	1,487(0.098)	14,963 (1.29)
	1977	*HF*	29,395	5,850(0.199)	22,002 (33.60)
	1977	*HM*	20,809	2,797(0.134)	16,894 (23.17)
	1980	*AI*	12,252		14,224(−13.87)
	1983	*AI*	13,178		14,672(−10.18)
	1983	*TR*	18,025		15,919 (13.23)
Albatross Rock IS	1972	*AI*	3,719		3,392 (9.63)
	1977	*AI*	2,461		4,235(−41.88)
	1977	*TR*	5,586	927(0.166)	4,594 (21.58)
	1977	*HM*	5,577	1,208(0.217)	5,188 (7.51)
	1977	*HF*	7,679	1,015(0.132)	6,756 (13.66)
	1980	*AI*	4,632		4,837 (−4.24)
	1983	*AI*	5,254		5,525 (−4.91)
	1983	*TR*	6,955		5,995 (16.02)
Sinclair Island IS	1972	*AI*	15,771		13,714 (15.00)
	1977	*AI*	11,066		11,763 (−5.93)
	1978	*AI*	9,587		11,408(−15.96)
	1978	*TR*	11,931	1,015(0.085)	12,378 (−3.61)
	1978	*HF*	15,910	918(0.058)	18,201(−12.59)
	1978	*HM*	15,083	895(0.059)	13,976 (7.92)
	1980	*AI*	11,370		10,729 (5.98)
	1983	*AI*	9,419		9,785 (−3.74)
	1983	*TR*	12,589		10,617 (18.58)
Elephant Rock IS	1972	*AI*	2,494		1,702 (46.56)
	1976	*AI*	1,630		1,471 (10.82)
	1976	*TR*	1,196	153(0.128)	1,596(−25.06)
	1976	*HM*	1,548	223(0.144)	1,802(−14.09)
	1976	*HF*	1,441	123(0.085)	2,347(−38.60)
	1977	*AI*	1,538		1,418 (8.44)
	1980	*AI*	1,826		1,271 (43.62)
Robbesteen IS	1972	*AI*	2,425		2,679 (−9.48)
	1977	*AI*	1,311		1,005 (30.41)
	1980	*AI*	473		558(−15.29)
Seal Island	1971	*AI*	14,449		14,148 (2.13)
False Bay IS	1971	*TR*	12,594	3,671(0.291)	15,351(−17.96)
	1971	*HM*	14,072	1,022(0.073)	17,332(−18.81)
	1971	*HF*	33,097	6,232(0.188)	22,572 (46.63)
	1977	*AI*	12,312		11,071 (11.21)
	1980	*AI*	8,188		9,793(−16.39)
	1982	*AI*	8,574		9,025 (−4.99)
	1982	*TR*	9,611	919(0.096)	9,792 (−1.85)
	1983	*AI*	10,017		8,663 (15.63)
Geyser Rock IS	1972	*AI*	2,679		3,525(−24.01)
	1976	*AI*	4,681		4,577 (2.28)
	1976	*TR*	6,533	845(0.129)	4,966 (31.56)
	1977	*AI*	6,873		4,885 (40.69)
	1980	*AI*	4,099		5,942(−31.01)
	1982	*AI*	6,139		6,770 (−9.32)
	1982	*TR*	8,163	1,423(0.174)	7,346 (11.13)
Quoin Rock IS	1972	*AI*	3,744		3,176 (17.87)
	1975	*AI*	1,730		1,670 (3.61)
	1975	*TR*	2,292	207(0.090)	1,812 (26.51)
	1975	*HM*	1,740	196(0.113)	2,046(−14.94)
	1975	*HF*	1,832	207(0.113)	2,664(−31.23)
	1977	*AI*	1,092		1,088 (0.41)
	1980	*AI*	630		572 (10.19)
Seal Island	1972	*AI*	3,234		3,616(−10.57)
Mossel Bay IS	1975	*AI*	1,262		1,640(−23.07)
	1975	*HM*	2,552	202(0.079)	2,010 (26.99)
	1975	*HF*	2,421	266(0.110)	2,617 (−7.50)
	1975	*TR*	2,095	298(0.142)	1,780 (17.71)
	1977	*AI*	1,177		968 (21.53)
	1980	*AI*	380		439(−13.50)
Hollams Bird	1972	*AI*	5,039		5,039 (0.00)
Island IU	1977	*AI*	2,807		2,807 (0.00)
Black Rock IU	1977	*AI*	221		221 (0.00)
	1980	*AI*	278		278 (0.00)
Jacobs Reef IU	1972	*AI*	4,804		4,804 (0.00)
	1977	*AI*	3,840		3,840 (0.00)
Black Rocks	1972	*AI*	1,702		1,074 (58.41)
Algoa Bay IU	1977	*AI*	112		382(−70.67)
	1980	*AI*	442		205 (115.26)

exponential form, but there is insufficient data to warrant the associated additional parameters, and the exponential should nevertheless produce a reasonable representation of the average trend for the short period concerned.

Hence the model underlying the estimation procedure is that if colony c produced N_c (0) pups in the initial year (taken to be 1971), then t years later N_c^* (t) pups will be produced, where

$$N_c^*(t) = N_c(0)\, e^{r_c t} \tag{1}$$

If method m is used t years after 1971 to assess the number of pups in colony c, the expected result will be

$$N_{m,c}^{\exp}(t) = B_m\, N_c(0)\, e^{r_c t} \tag{2}$$

The model has $M + 2C = 51$ parameters in all: 5 method bias factors and 2×23 colony population parameters (initial sizes and increase rates). Clearly the data can determine only relative and not absolute bias factors, so that B_1 (corresponding to the *TR* method) was set equal to 1. (This is discussed further in a subsequent section.)

To estimate the remaining $M + 2C - 1 = 50$ parameters from the $n = 132$ colony size assessments $N_{m,c}^{\text{obs}}(t)$ available, it was assumed that

$$N_{m,c}^{\text{obs}}(t) = N_{m,c}^{\exp}(t)e^{\varepsilon} \qquad \varepsilon \text{ from } N(0,\sigma^2)$$

$$= B_m N_c(0) e^{r_c t+\varepsilon} \tag{3}$$

where the errors ε are normally distributed with mean 0 and standard deviation σ.

Note that σ will reflect a combination of assessment error, σ (method), and model error, σ (model):

$$\sigma^2 = \sigma^2 \text{ (method)} + \sigma^2 \text{ (model)} \tag{4}$$

The estimation procedure assumes σ^2 (method) is the same for the various assessment methods (m). (This is discussed further in Appendix A2.) Maximum likelihood parameter estimation then corresponds to the least squares minimization of

$$\sum_{m,c,t} [\ell n\, N_{m,c}^{\text{obs}}(t) - \ell n\, B_m - \ell n\, N_c(0) - r_c t\,]^2 \tag{5}$$

The solution was found computationally. Associated values of the expected assessments results $N_{m,c}^{\exp}(t)$ are shown in Table 1, together with the percentage discrepancies to which actual assessments $N_{m,c}^{\text{obs}}(t)$ correspond. For five of the colonies (Van Reenen Bay, Lions Head, Hollam's Bird Island, Black Rock, and Jacobs Reef) only two observations are available in each case; thus the model (equation (1)) fits exactly and the discrepancies are zero. More technical aspects of the calculation procedures, including further discussion of the assumptions made and the method used to estimate standard errors, are detailed in Appendix A.

Results and discussion

Table 2 shows estimates of initial pup population size $N_c(0)$ (referring to the year 1971) and annual increase rates for each colony. The increase rate r_c has been expressed as a percentage growth per annum R_c as follows:

Table 2—Pup population size estimates for each fur seal colony in 1971 and 1983 together with the annual growth rate (equation (6)). The parenthesized figures are standard errors followed, in the case of population sizes, by coefficient of variation estimates. Population sizes are in terms of the *TR* assessment method.

Colony	Pup population 1971	Pup population 1983	Annual growth (%)
Cape Cross	25,493(7,308/0.287)	19,782 (3,734/0.189)	−2.09(3.22)
Wolf Bay	15,184(4,760/0.313)	37,943(11,227/0.296)	7.93(4.76)
Atlas Bay	27,975(5,756/0.206)	87,518(19,876/0.227)	9.97(3.48)
Kleinsee	29,185(4,246/0.145)	95,283(15,063/0.158)	10.36(2.20)
Van Reenen Bay	4,103(1,130/0.275)	4,786 (1,720/0.359)	1.29(3.98)
Lions Head	3,433(1,143/0.333)	5,107 (3,933/0.770)	3.37(6.81)
Marshall Reef	1,015 (301/0.297)	117 (42/0.359)	−16.50(3.96)
Staple Rock	3,774(1,081/0.286)	1,380 (359/0.260)	−8.04(3.66)
Boat Bay Rock	2,293 (619/0.270)	467 (133/0.285)	−12.42(3.50)
Dumfudgeon Rock	3,440 (934/0.272)	257 (66/0.257)	−19.45(3.05)
Long Islands	14,064(2,771/0.197)	15,919 (2,362/0.148)	1.04(2.46)
Albatross Rock	3,521 (764/0.217)	5,995 (855/0.143)	4.53(2.57)
Sinclair Island	15,344(3,310/0.216)	10,617 (1,444/0.136)	−3.02(2.36)
Elephant Rock	1,915 (485/0.253)	1,237 (392/0.317)	−3.58(3.91)
Robbesteen	3,536 (966/0.273)	336 (110/0.327)	−17.80(3.33)
Seal Island False Bay	15,351(1,872/0.122)	9,400 (1,303/0.139)	−4.00(1.48)
Geyser Rock	3,583 (744/0.208)	7,841 (1,373/0.175)	6.74(2.72)
Quoin Rock	4,270 (835/0.196)	326 (110/0.337)	−19.29(3.04)
Seal Island Mossel Bay	5,107(1,026/0.201)	216 (69/0.319)	−23.16(2.90)
Hollams Bird Is	6,146(1,884/0.307)	1,509 (1,089/0.722)	−11.04(5.71)
Black Rock	152 (182/1.197)	379 (246/0.649)	7.95(12.20)
Jacobs Reef	5,451(1,603/0.294)	3,184 (2,441/0.767)	−4.38(6.01)
Black Rocks Algoa Bay	1,434 (384/0.268)	120 (39/0.325)	−18.69(3.22)

$$R_c = 100(e^{r_c} - 1) \tag{6}$$

Standard error and coefficient of variation estimates are also shown; these have been derived as detailed in Appendix A3.

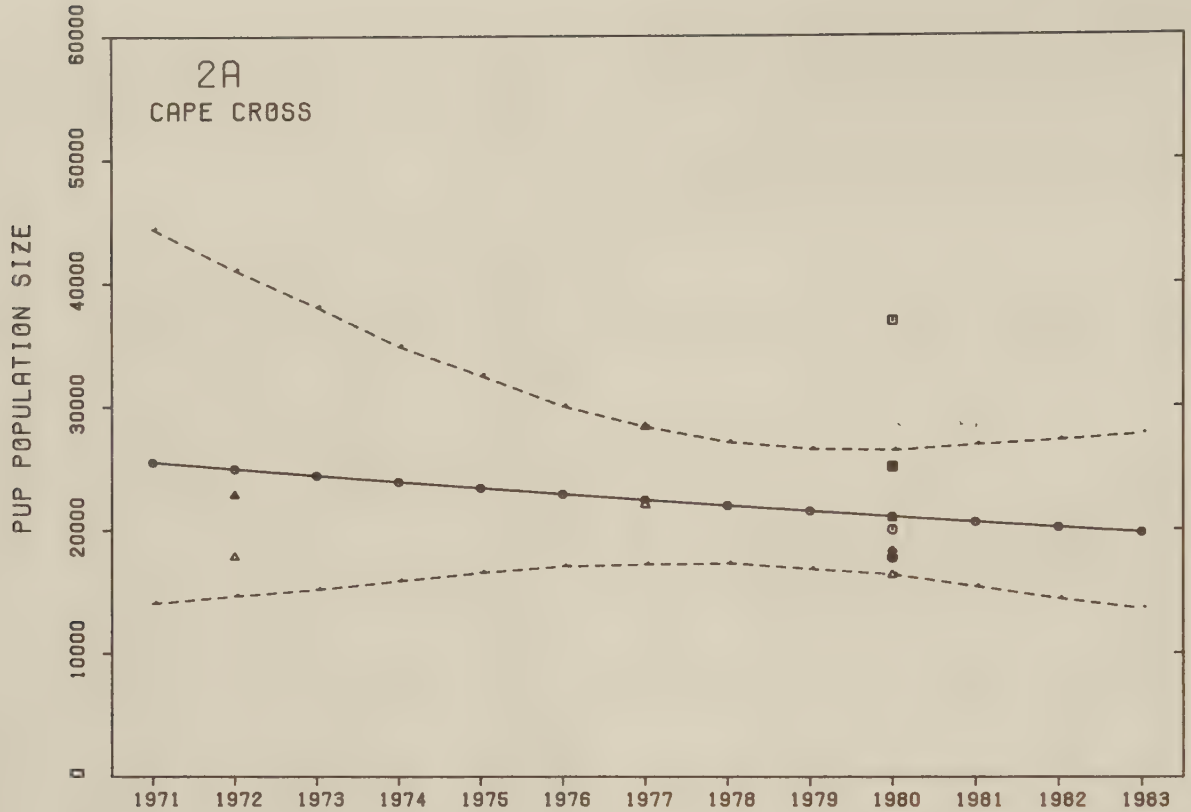
Population size estimates for 1983 have been calculated from

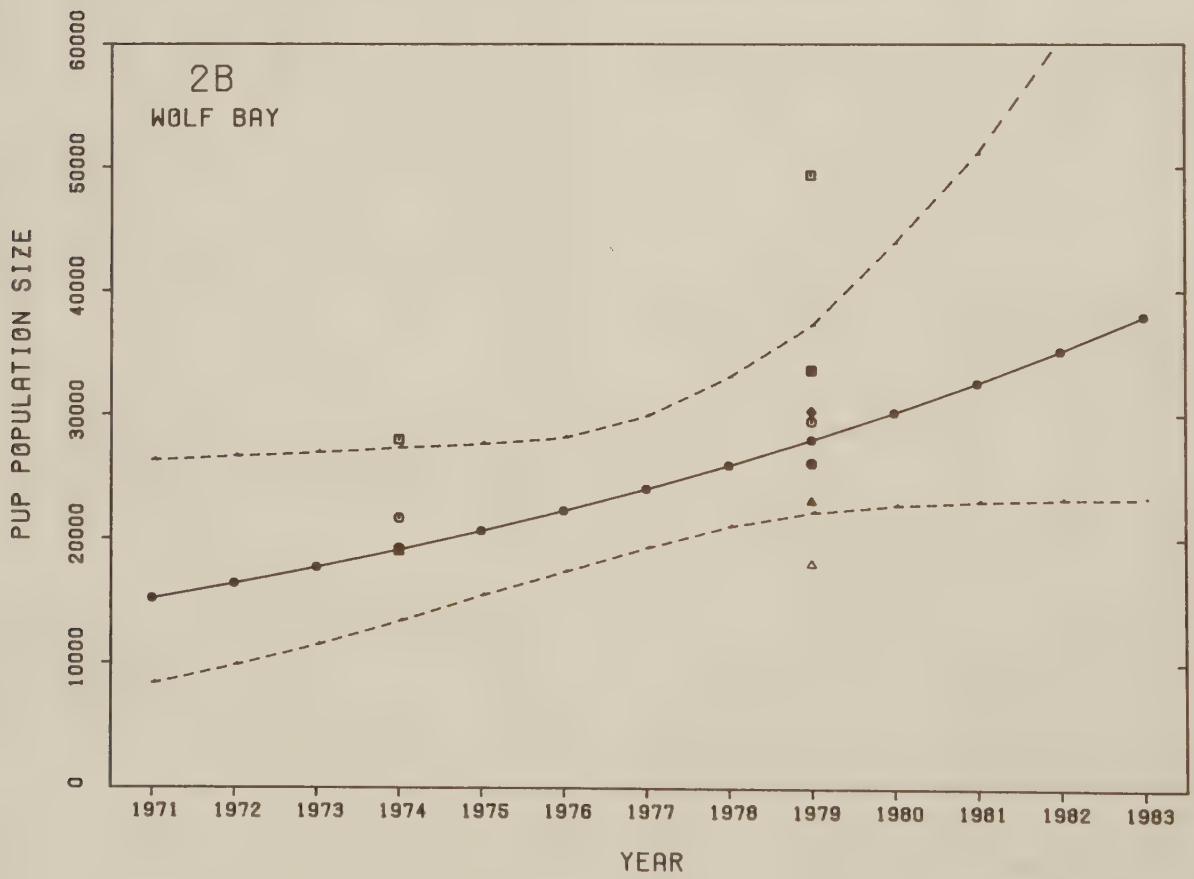
$$N_c(12) = N_c(0)e^{12r_c} \tag{7}$$

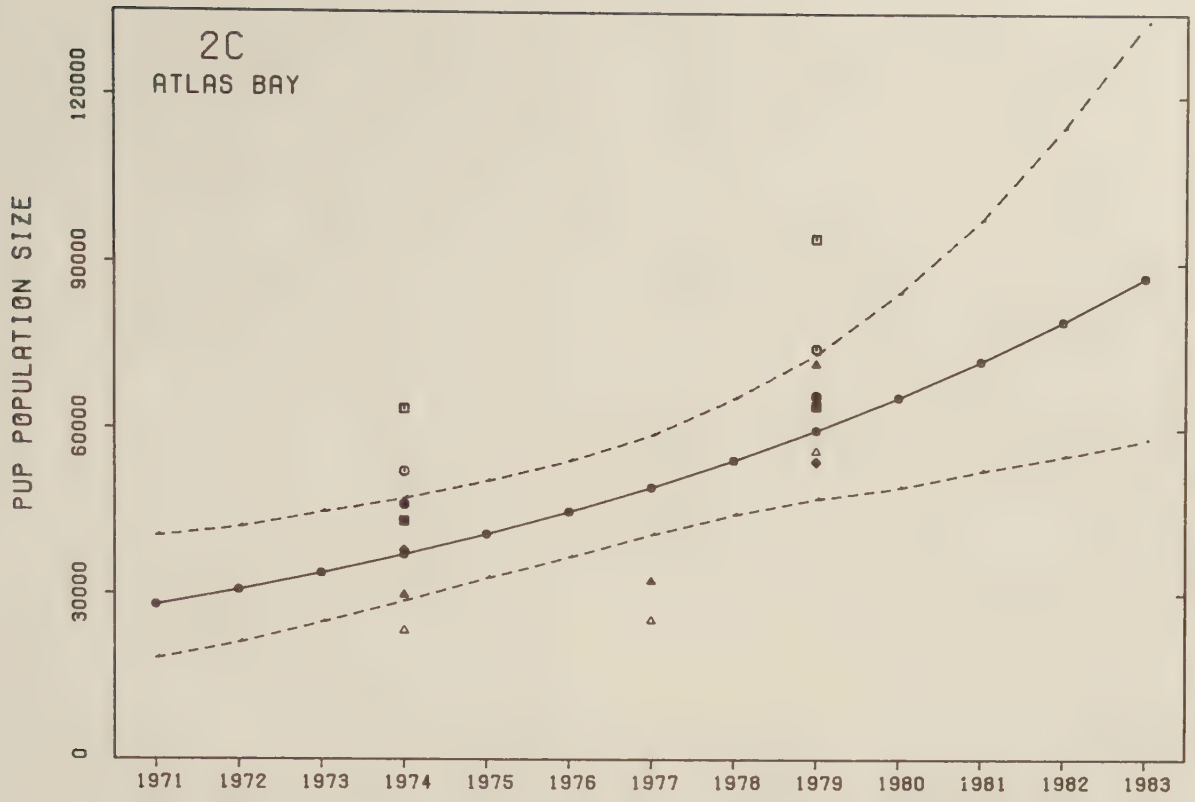
All population estimates shown are normalized to the *TR* assessment method. Thus, for the purpose of presentation at this stage, this particular method is assumed to provide unbiased assessments.

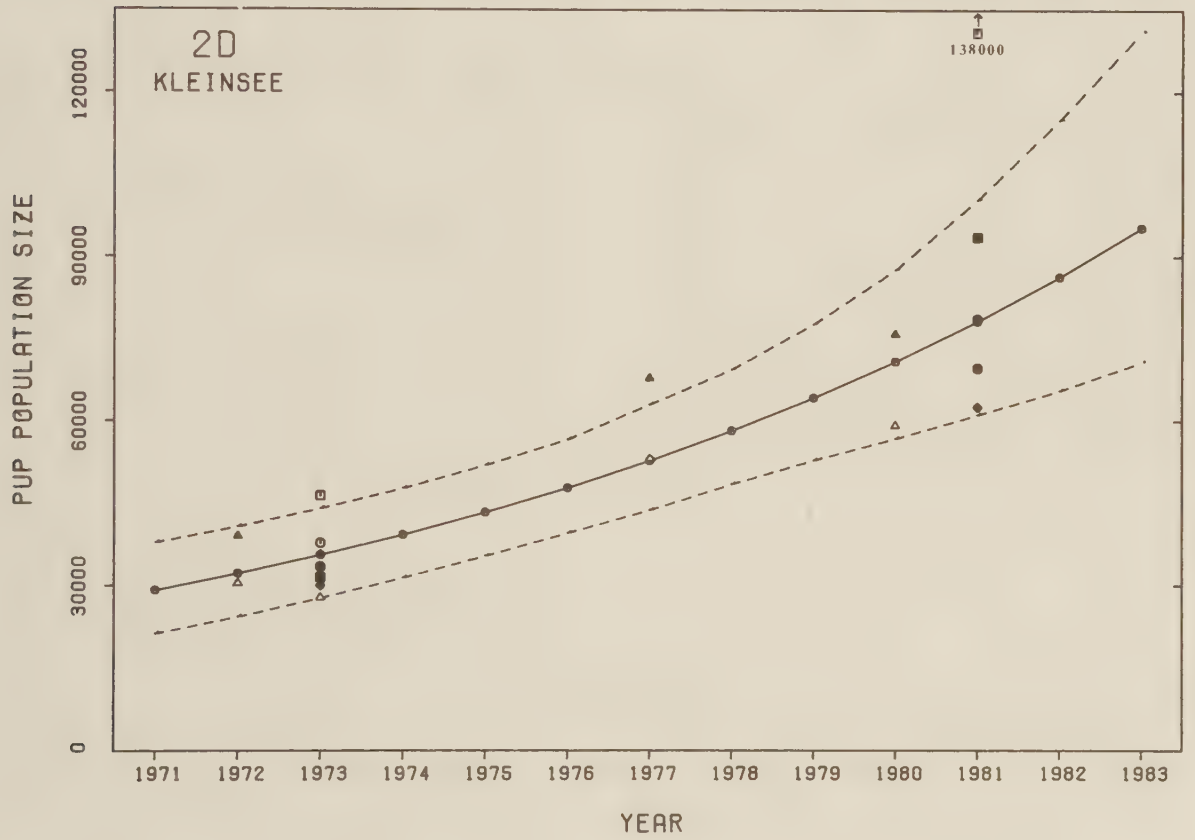
Figure 2 shows the actual assessments and estimated population trends for a number of colonies. Figures 2 a-d show the four colonies (all mainland) that make up the bulk of the population: Cape Cross,

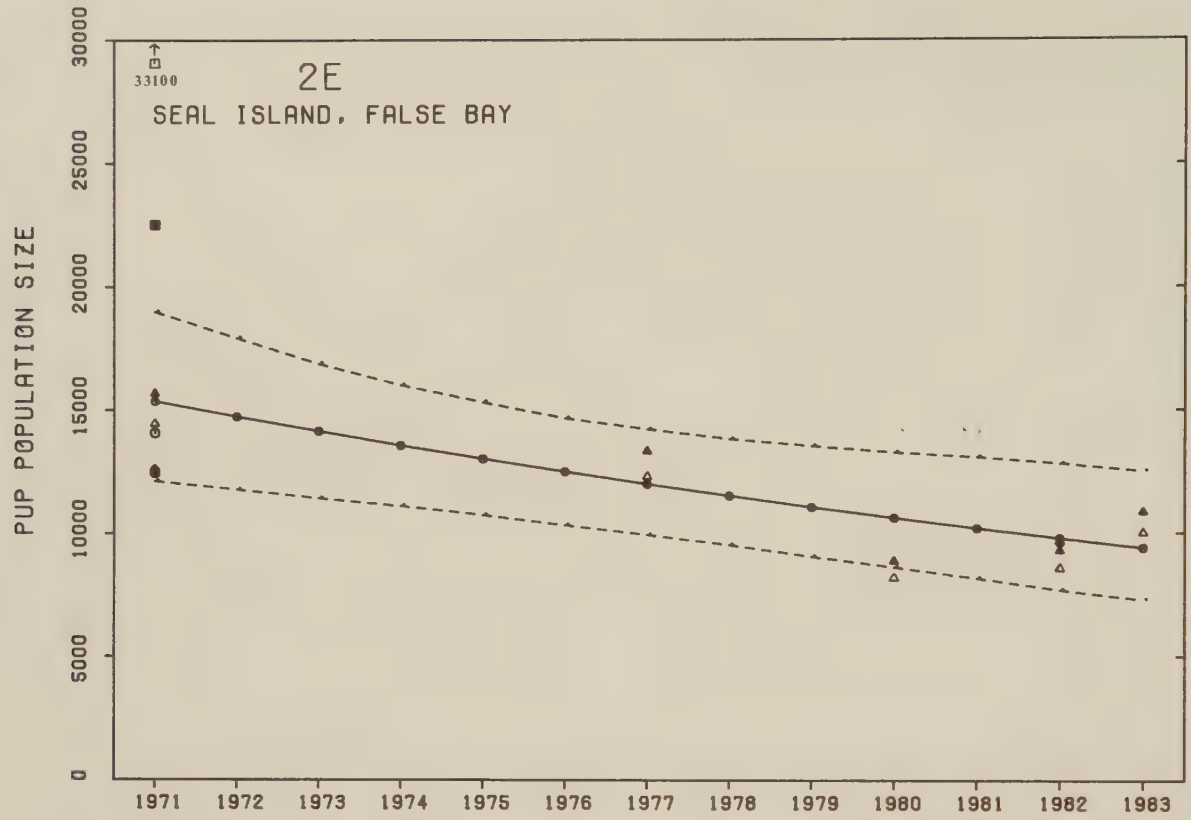
Figure 2—Model estimates of pup population sizes (normalized to the *TR* assessment method) at (a) Cape Cross, (b) Wolf Bay, (c) Atlas Bay, (d) Kleinsee, (e) Seal Island False Bay, and (f) Geyser Rock from 1971 to 1983 are shown (•) and are joined by solid straight lines. Corresponding 95% confidence intervals for these estimates are shown joined by dashed straight lines. Actual assessments are indicated by open symbols, while corresponding closed symbols show those same assessments adjusted for bias relative to the *TR* method: *TR* (⧫); *AM/AI* (△/▲); *HM* (○/●); *HF* (□/■).


2A
CAPE CROSS
PUP POPULATION SIZE
0
10000
20000
30000
40000
50000
60000
1971
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
1982
1983


2B
WOLF BAY
PUP POPULATION SIZE
0
10000
20000
30000
40000
50000
60000
1971
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
1982
1983
YEAR


2C
ATLAS BAY
PUP POPULATION SIZE
0
30000
60000
90000
120000
1971
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
1982
1983


2D
KLEINSEE
138000
PUP POPULATION SIZE
0
30000
60000
90000
120000
1971
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
1982
1983
YEAR


2E
SEAL ISLAND, FALSE BAY
33100
PUP POPULATION SIZE
0
5000
10000
15000
20000
25000
30000
1971
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
1982
1983

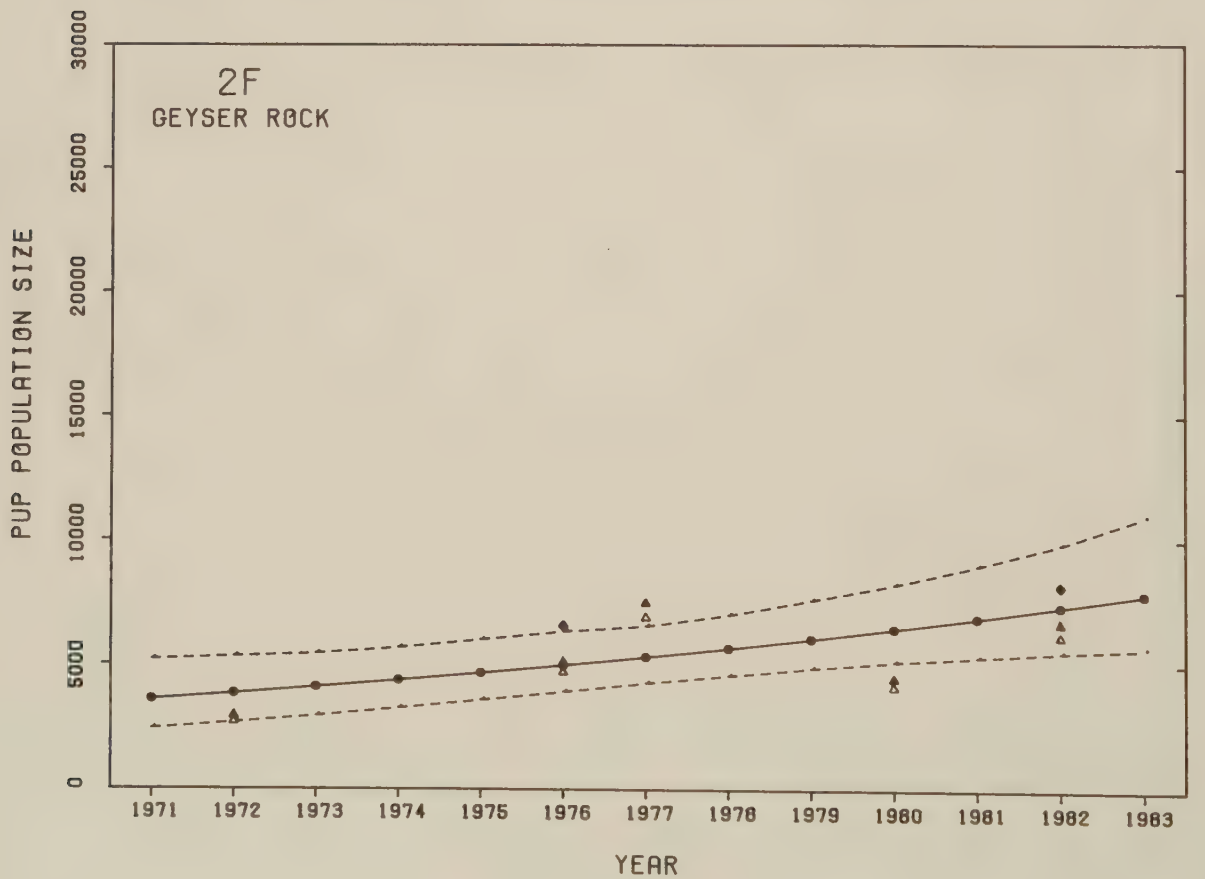

2F
GEYSER ROCK
PUP POPULATION SIZE
0
5000
10000
15000
20000
25000
30000
1971
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
1982
1983
YEAR

Table 3—Bias factors B_m (equation (2)) for the various assessment methods calculated using expression (5). The bias factor for the *TR* method was taken to be 1. Standard errors have been evaluated as indicated in Appendix A3 expressions (A6/A7). Comparative assessments refer to ratios of the assessment for the method concerned compared with that for the *TR* assessment in cases where more than one method was used for the same colony in the same year, as detailed in Appendix A1.

Assessment method	Model		Comparative assessments		
	B_m	SE	Avg.	SE	SD (C.V.)
TR	1	—	—	—	—
AM	0.780	0.080	0.783	0.096	0.216(0.276)
AI	0.922	0.059	0.892	0.066	0.274(0.308)
HM	1.129	0.085	1.190	0.045	0.176(0.148)
HF	1.470	0.114	1.601	0.124	0.479(0.299)

Wolf Bay, Atlas Bay, and Kleinsee. Also shown (Figs. 2 e-f) are two of the larger island colonies: one decreasing (Seal Island, False Bay) and one increasing (Geyser Rock).

The bias factors B_m (equation (2)), estimated by the minimization procedure together with their associated standard errors, are shown in Table 3. The factor for the *HF* method is 30% higher than that for *HM* (significantly so: $P < 0.01$). This was anticipated from observations of higher male/female ratios among tagged pups relative to untagged at harvest.

Both *HM* and *HF* bias factors are higher than for *TR* (although the excess for *HM* is marginally nonsignificant: $P = 0.06$). In all probability, differential mortality between tagged and untagged pups positively biases both *HM* and *HF* assessments. Tag-recapture assessments, on the other hand, may be negatively biased because of incomplete mixing of tagged and untagged pups among the colony as a whole prior to recapture, combined with a tendency for recapture stations to be in the same areas where the pups were tagged due to the difficult terrain, which makes it impossible to herd pups in certain areas.

The bias factors for the aerial method are smaller than for the *TR* method (although not significantly so for *AI*, $P = 0.11$; whereas for *AM*, $P = 0.01$). The aerial assessments generally take place earlier and therefore some of the counted pups die before the time of *TR* assessments. However, this is conceivably overcompensated by missing pups in the aerial photographs because some animals are hidden under rocks or in shadows, or undercounted due to being massed in dense clumps.

The only surprising feature is the smaller B_m value for mainland as opposed to island aerial censuses. A greater proportion of pups would be expected to be hidden on the rockier islands. The smaller mainland value borders on statistical significance ($P = 0.06$). Without the anomalous aerial censuses of the four Luderitz Bay colonies in 1978 (Appendix A1), however, the B_m values for *AM* and *AI* methods would be virtually identical.

The estimation of σ is detailed in Appendix A2 (equation (A3)), and yields a value

$$\sigma = 0.232$$

This corresponds to a root mean square error of approximately 24% in model estimates of pup population size compared with actual assessment values. These differences comprise not only sampling error in the assessment procedures which for the tag-recapture assessments average 14% (coefficient of variation). Assuming this

Table 4—Fur seal pup population sizes in 1971 and 1983 and annual growth rates for various colony combinations. The parenthesized figures are standard error followed by C.V. estimate. Population sizes are in terms of the *TR* assessment method.

Colony combination	Pup population		Annual growth (%)
	1971	1983	
Mainland harvested	97,836(12,406/0.127)	240,526(28,975/0.120)	7.78(1.63)
Mainland unharvested	7,536(1,651/0.219)	9,893(4,383/0.443)	2.29(3.94)
Island harvested	77,211(6,336/0.082)	54,107(4,159/0.077)	−2.92(0.90)
Island unharvested	13,182(2,688/0.204)	5,193(2,689/0.518)	−7.47(3.96)
Mainland	105,372(12,938/0.123)	250,419(29,220/0.117)	7.48(1.54)
Island	90,393(7,588/0.250)	59,300(5,036/0.085)	−3.45(0.93)
North of Orange River	125,935(13,404/0.106)	191,775(25,453/0.133)	3.57(1.55)
South of Orange River	69,831(5,688/0.081)	117,943(15,604/0.132)	4.46(1.39)
All colonies	195,766(15,993/0.082)	309,719(30,303/0.098)	3.90(1.08)

is an appropriate value for σ (method), and taking this to be the same for all methods, equation (4) then gives

$$\sigma \text{ (model)} \approx \sqrt{0.232^2 - 0.14^2} = 0.185$$

which corresponds to a root mean square error of about 19%, so that σ (model) appears the dominant contributor to σ^2. This result is not altogether surprising. Other effects would be expected to contribute to the overall variation and are further discussed in Appendix A3.

This does suggest, however, that in respect of monitoring a general trend in the population size, it is not necessary to obtain individual colony assessments with great precision (e.g., doubling the sampling intensity for tag-recapture asssessments would achieve only a 10% increase in the precision of estimates of such trend).

Table 4 shows size and increase rate estimates for various combinations of colonies. The annual percentage growth rate in these cases has been estimated from the sum of pup population estimates for the colonies concerned in 1971 and 1983:

$$R = 100 \left\{ \left[\frac{\sum_c N_c(12)}{\sum_c N_c(0)} \right]^{1/12} - 1 \right\} \qquad (8)$$

Broadly, the results reflect a decrease in the island colony populations, but an increase in the mainland colonies. Overall the annual growth is nearly 4% per annum over the 1971-83 period. This is a consequence of high increase rates at the three largest mainland colonies: Wolf Bay, Atlas Bay, and Kleinsee, which together comprise 71% of the total 1983 pup population estimate.

An apparent anomalous feature of these results is that harvested colonies appear to be increasing faster (mainland) or decreasing less quickly (island) than unharvested colonies. However, there have been relatively few assessments of the unharvested colonies, so that the standard errors for their increase rates are large, and the differences noted are not significant ($P = 0.13$ and $P = 0.16$, respectively).

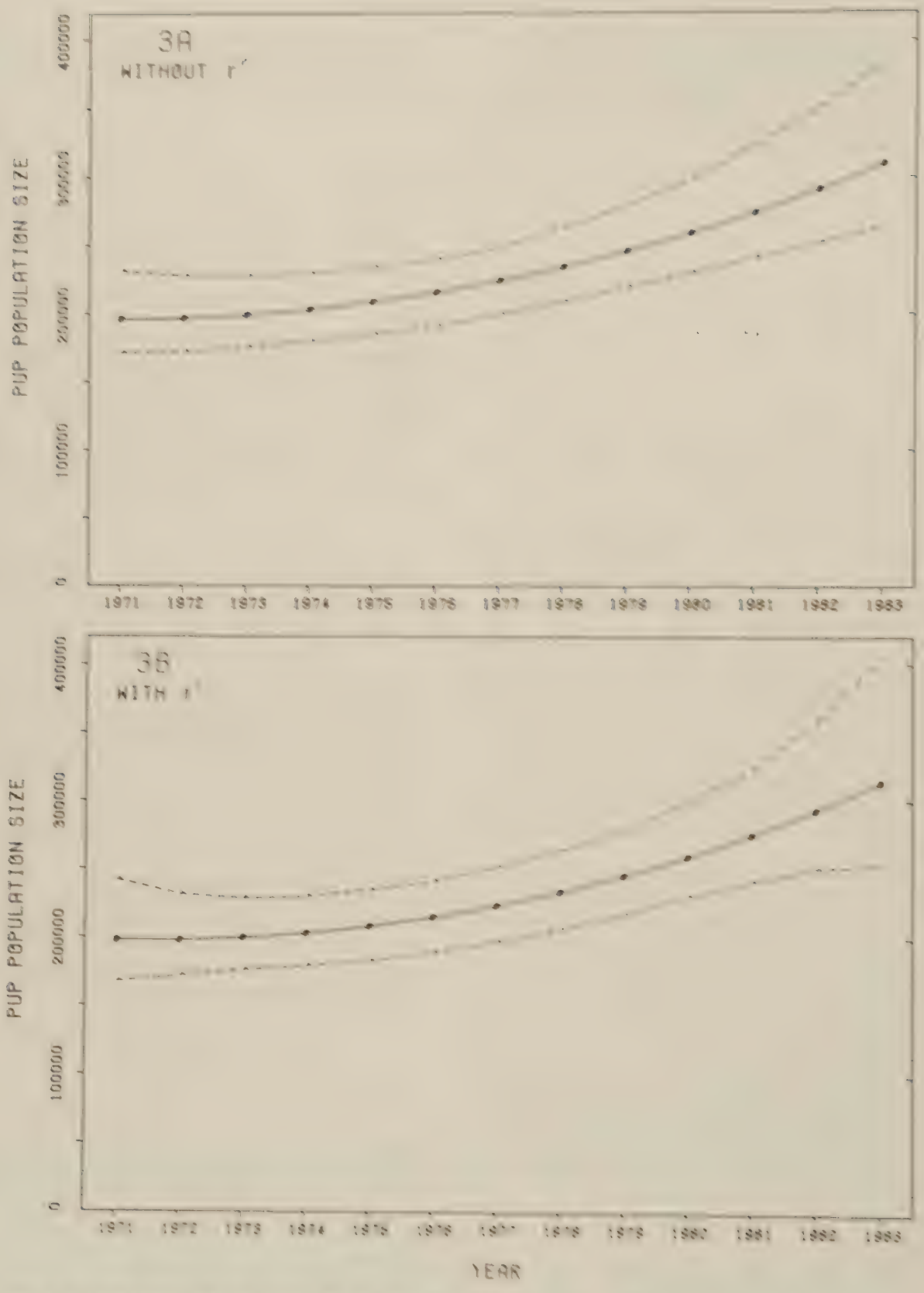


Figure 3 –(a) Model estimates of pup populations for all colonies combined for the years 1971 to 1983 are shown (•) and are joined by solid straight lines. Corresponding 95% confidence intervals for these estimates are shown joined by dashed straight lines. (b) A population growth model incorporating the r' parameter (equation (10)).

Table 5—Annual percentage growth rates (R) for all colonies combined for various periods.

	Basic model (eq. 2)			Model with r' (eq. 10)		
Period	R	SE	Prob. < 0	R	SE	Prob < 0
1971-83	3.90	1.08	<0.01	3.94	1.10	<0.01
1971-72	0.42	0.92	0.59	−0.04	2.68	0.60
1976-78	4.21	1.12	<0.01	4.25	1.14	<0.01
1982-83	6.46	1.55	<0.01	7.04	3.52	0.02
Change from 1971-72 to 1982-83						
	6.05	1.44	<0.01	7.08	5.85	0.07

While the model estimates the average annual growth rate of 4% over the period concerned with fair precision (SE 1%), an important consideration for current management decisions is the magnitude of the present growth rate. Density-dependent effects might be expected to slow the overall growth rate as the population size increases.

Figure 3a shows the estimates of overall pup population size on an annual basis, obtained by summing the estimates for each colony each year. From this (and Table 5), it might appear that there is a significant increase in the overall growth rate from 1971 to 1983.

However, that may be an artifact of the exponential model used to represent colony growth trends (equation (1)). The fact that the largest colonies have increased over the period while the smaller ones have mainly decreased would tend to produce an increasing growth rate when results for the individual colonies are combined.

To compensate for such a possible effect, it is desirable to incorporate some allowance for changing growth rates in the model. However, given the large amount of noise in the data and the small number of data points for many of the colonies, there would clearly be little point in attempting to estimate colony-specific changes in increase rates, for example by a model of the form

$$N_c^*(t) = N_c(0)e^{r_c t + r_c' t^2} \tag{9}$$

which would introduce an additional 23 parameters (or, more correctly, 18, since for five of the colonies only 2 data points are available, making r_c' indeterminate for those colonies).

Thus a simpler form was attempted, taking r' to be the same for all colonies so that only one extra parameter was introduced:

$$N_{m,c}^{\exp}(t) = B_m N_c(0)e^{r_c t + r' t^2} \tag{10}$$

In a colony-specific sense, it is biologically unrealistic to assume r' to be colony-invariant. However as discussed earlier (preceding equation (1)), the primary motivation for the growth model chosen is simple representation of trends. The r' parameter should therefore be considered as a total population trend parameter (relating only indirectly to individual colonies), that has been introduced to allow greater flexibility of choice of overall trends by the model fitting procedure.

The results arising from fitting this alternative model are shown in Figure 3b and Table 5. The estimate for the parameter r' is

$$r' = 0.00046 \text{ yr}^{-2} \text{ (SE } 0.00250)$$

Though a positive value is not what might be expected biologically, the relatively large standard error shows that the available data cannot estimate this parameter with any reasonable precision.

The estimated change in growth rate over the period concerned increases slightly from 6% to 7% with the introduction of r'. However, the standard error of the estimate increases sharply to 6%, so that the change is no longer significantly positive ($P = 0.07$), as appeared to be the case with the original model (equation (2)). If time changes rather than averages for the total pup population over the 1971-83 period are to be considered, the confidence intervals in Figure 3b (with r' incorporated) would seem a more realistic representation that those of Figure 3a.

MODELING THE POPULATION DYNAMICS

The basic model

The number of female seals having reached the age of first parturition (η) in year ($t + 1$) is given by the following equation

$$\eta_{t+1} = \eta_t S_a + (\eta_{t-3}\, \rho\, q_f s_{10} s_{11} - C_{t-3} q_{fh})\, s_{12} s_2 s_3 s_4 \tag{11}$$

where

$S_a = e^{-M_a}$ = average annual survival rate for female seals after reaching the age of first parturition
s_{10} = survival rate of female pups between time of birth and tagging
s_{11} = survival rate of female pups between time of tagging and harvesting
s_{12} = survival rate of female pups between harvesting and first birthday
$s_2/s_3/s_4$ = survival rate of juvenile females in their second/third/fourth year of life
ρ = pregnancy rate
q_f = fraction of pups born that are female
q_{fh} = fraction of pups harvested that are female
C_t = number of pups harvested in year t.

Equation (11) assumes the age at first parturition of Cape fur seals is 4 years. Data in Shaughnessy (1982) indicate that this age is greater than 3 years. By way of comparison, the average age at first reproduction of northern fur seals is often as late as 5 or 6 years (C. Fowler and A. York, Natl. Mar. Mammal Lab., Seattle, pers. commun.).

Equation (11) may be rewritten

$$\eta_{t+1} = \eta_t S_a + \eta_{t-3}\left[1 - \frac{C_{t-3}}{\eta_{t-3}\rho\, s_{10}} \frac{q_{fh}}{q_f s_{11}}\right] \rho\, q_f s_{10} s_{11} s_{12} s_2 s_3 s_4$$

$$= \eta_t S_a + \eta_{t-3}(1 - F_{t-3})\,\lambda \tag{12}$$

where $F = \dfrac{C}{\eta\, \rho\, s_{10}} \dfrac{q_{fh}}{q_f s_{11}}$ (13)

$$\lambda = \rho\, q_f s_{10} s_{11} s_{12} s_2 s_3 s_4$$

The variable F represents the proportion of the female pups culled at the time of harvesting, and so is referred to as a harvesting rate.

If the population is increasing (or decreasing) with a steady annual growth rate of R (no longer expressed as a percentage; cf. equation (6)), then

$$\eta_{t+1} = (1 + R)\eta_t = (1 + R)^4 \eta_{t-3} \tag{14}$$

Assuming constancy in the biological parameters (i.e., neglecting any density dependence, among other factors), and taking the harvesting rate F to be fixed, equations (12) and (14) then give

$$(1 + R)^4 = (1 + R)^3 S_a + \lambda(1 - F) \qquad (15)$$

Initial parameter probability distributions

The following prior information is available for the four parameters R, F, S_a, and λ in equation (15).

Annual growth rate (R)—The procedures indicated by expressions (A6) and (A7), together with equation (8), provide a probability distribution for R.

Harvesting rate (F)—The number of pups present at the time of tagging is related to the number of adult females by the expression

$$N_{TR} = \eta \rho s_{10} \qquad (16)$$

In estimating F, $\eta \rho s_{10}$ was taken to be $\mu \overset{\text{est}}{N}_{TR}$. The value $\overset{\text{est}}{N}_{TR}$ is the average of the pup population estimates for all colonies combined for the years 1971-83, assuming the *TR* assessment method is unbiased; expressions (A6) and (A7) provide a probability distribution for $\overset{\text{est}}{N}_{TR}$. The factor μ allows for possible bias in the *TR* method; it was taken to have a uniform distribution over the range 0.75 to 1.15. The extremes of this range correspond approximately to the bias factors for the *AM* and *HM* assessment methods (Table 3); it is considered reasonable to assume that the former method is definitely negatively biased because of hidden animals, while the latter is positively biased due to higher mortalities among tagged pups.

The value of C in the formula for F was taken to be the average annual harvest over the period concerned: 72,993 animals. The harvest was assumed to consist entirely of 0-year-old animals, though a small proportion of older animals has been taken occasionally.

The q_m, q_f ratio was taken to be unity. Observations suggest this may be slightly less than 1, but again adjusting for this scarcely seems warranted, given the coarseness of specifying μ.

The s_{11} factor is certainly bounded above by 1. This bound can be reduced by assuming that adult natural mortality is uniform throughout the year, and that any pup whose mother dies during the period of approximately 7 months between tagging and harvesting will also die. Thus s_{11} is bounded above by

$$e^{-7/12 \cdot M_a} = (S_a)^{7/12}$$

A lower bound for s_{11} is more problematic. Certainly a lower bound on the number of pups present at the time of harvest is the number harvested. For the Seal Island Mossel Bay colony in 1975, a harvest of 1,631 pups followed a *TR* assessment of 2,095 pups earlier in the year. The ratio 0.78 has been taken as a lower bound of s_{11} (admittedly ignoring statistical fluctuation for that particular *TR* assessment). Thus s_{11} was taken to have a uniform distribution (the simplest assumption in the absence of any further information) over the range 0.78 to $S_a^{7/12}$.

Convoluting the distributions of N_{TR}, μ, and s_{11} provides a probability distribution for F.

Average adult survival rate (S_a)—No age distribution data are available for the adult South African fur seal, so that an initial probability distribution for S_a has to be based on comparisons from other seal populations. Obviously S_a is bounded above by 1. The highest annual adult survival rate of those shown for various ages of the Pribilof population by Smith and Polacheck (1981) is 0.95, and this was taken as the upper bound for S_a. Following inspection of the Smith-Polacheck data, the lower bound for S_a was semi-arbitrarily taken to be 0.7. Thus S_a was taken to have a uniform distribution over the range 0.7 to 0.95. This corresponds to an M_a range 0.051 to 0.357, or an average lifespan after first parturition in the range 2.8 to 19.5 years.

For a stable population the Smith-Polacheck data correspond to an average adult survival rate of 0.84. As the South African fur seal population is expanding (Table 4), younger adults (with higher survival rates) will be over-represented in the population compared to a steady-state situation, so that a higher S_a than might be appropriate for an equilibrium situation would be anticipated.

Pregnancy and juvenile survival factor (λ)—An upper bound on λ has been estimated on the following basis:

ρ	$\leqslant 0.8$ (measured)
q_f	$\leqslant 0.45$ (measured)
$s_{10}s_{11}s_{12}$	$\leqslant S_a$ (assuming that if the mother dies during the pup's first year of life, the pup will die also)
$s_2/s_3/s_4$	$\leqslant 0.95$ (assuming that juvenile survival rates cannot be greater than the highest adult survival rate thought possible, viz: 0.95).

$$\text{Thus } \lambda_{\max} = 0.8 \times 0.45 \times S_a \times (0.95)^3 \qquad (17)$$

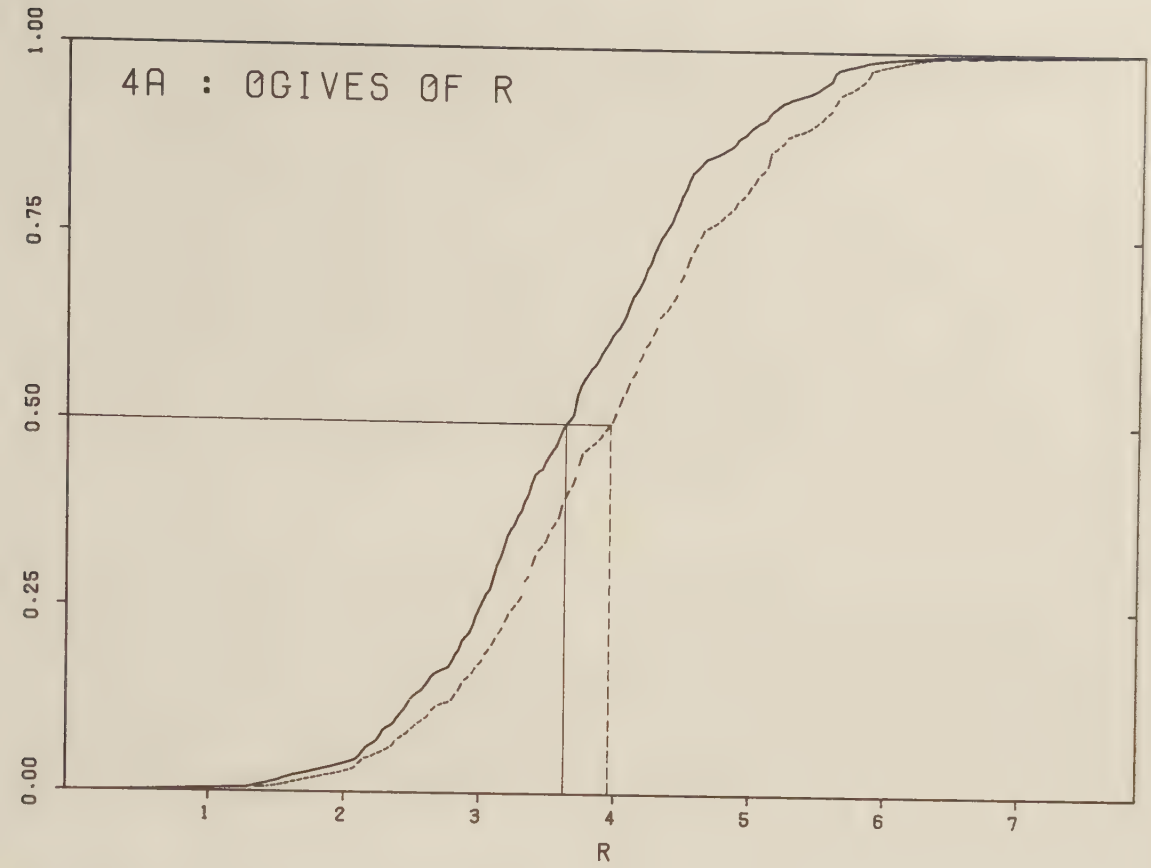
The parameter is assumed uniformly distributed over the range 0 to $\lambda_{\max}$. A non-zero lower bound for λ would have been desirable for the technique following, but no basis on which to set lower limits for the juvenile survival rates is apparent.

Refining the parameter probability distributions

Initial probability distributions (represented by ogives) for the parameters R, F, S_a, and λ as constructed in the previous sections, are shown in Figures 4a-d. As only 400 simulations were used to provide the R and N_{TR} values, regression techniques have been used to smooth the corresponding ogives shown.

The four parameters are subject to the constraint of equation (15). This constraint provides additional information on the parameters, and so allows the probability distributions of the previous section to be refined. In principle, the intent of this refinement was to generate values of R, F, S_a and λ from the distributions constructed in the previous section, and retain only those sets which satisfied equation (15). In practice this was achieved by generating three of the parameter values in this way, finding the value of the fourth that then satisfied equation (15), and then weighting (w) the resultant set of four parameter values according to the probability-density function previously constructed for that fourth parameter. This approach, and the sensitivity of its results to some of the assumptions of the previous section, are discussed in more detail in Appendix B.

One thousand such $\{R, F, S_a, \lambda, w\}$ sets satisfying equation (15) were generated. The 1,000 $\{S_a, w\}$ values, for example, then provide a refined probability distribution for S_a. These refined probability distributions (again smoothed using regression techniques) are also shown in ogive form in Figures 4a-d. This technique can also be used to provide refined probability distributions for



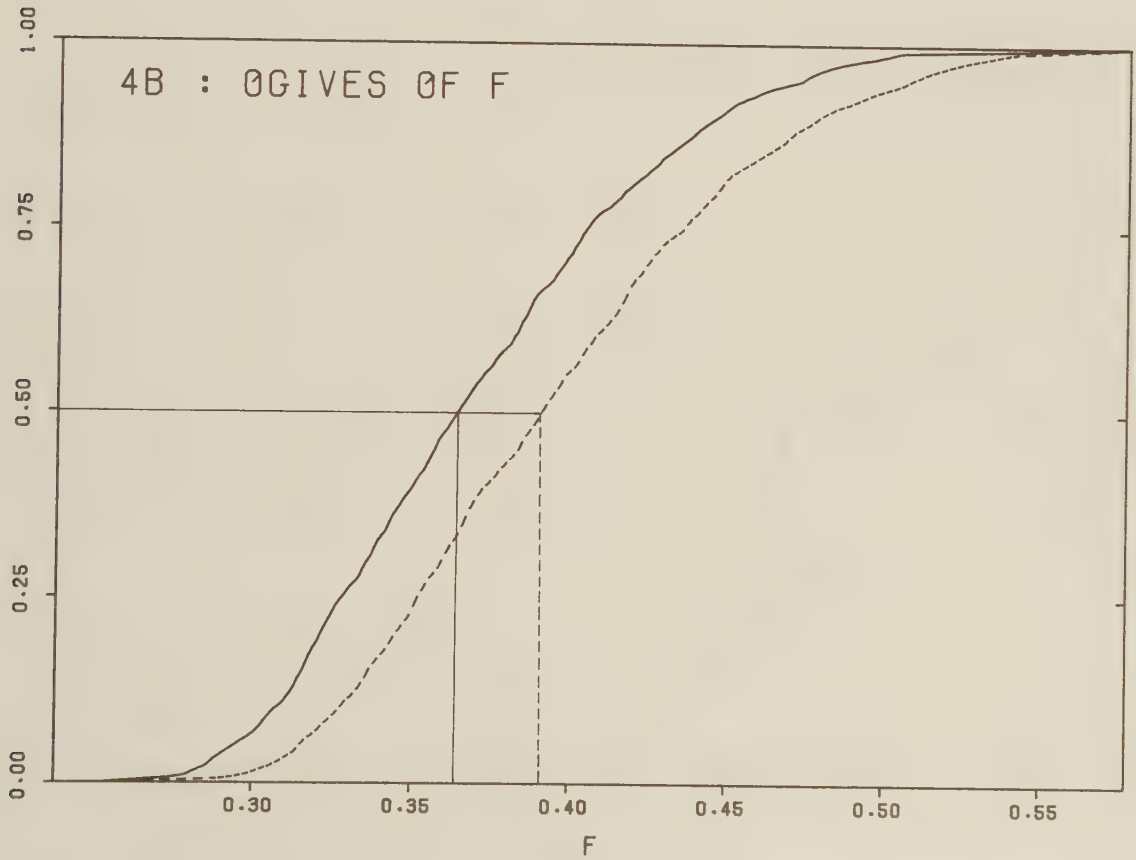
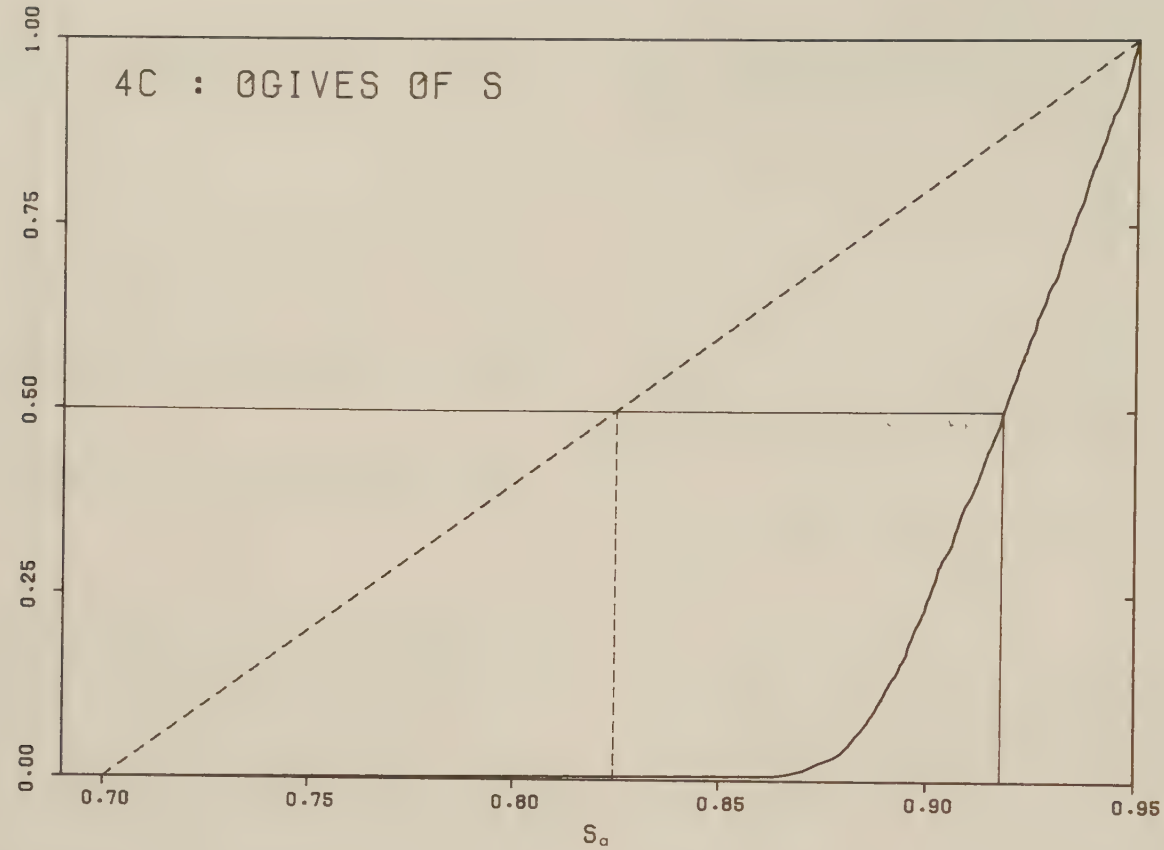


Figure 4—Probability distributions for population dynamics model parameters (a) R; (b) F; (c) S_a and (d) λ represented by ogives. The initial distributions are shown by dashed lines; the refined distributions (incorporating the equation (15) constraint) are shown by solid lines.


4C : 0GIVES 0F S
1.00
0.75
0.50
0.25
0.00
0.70
0.75
0.80
0.85
0.90
0.95
S_a

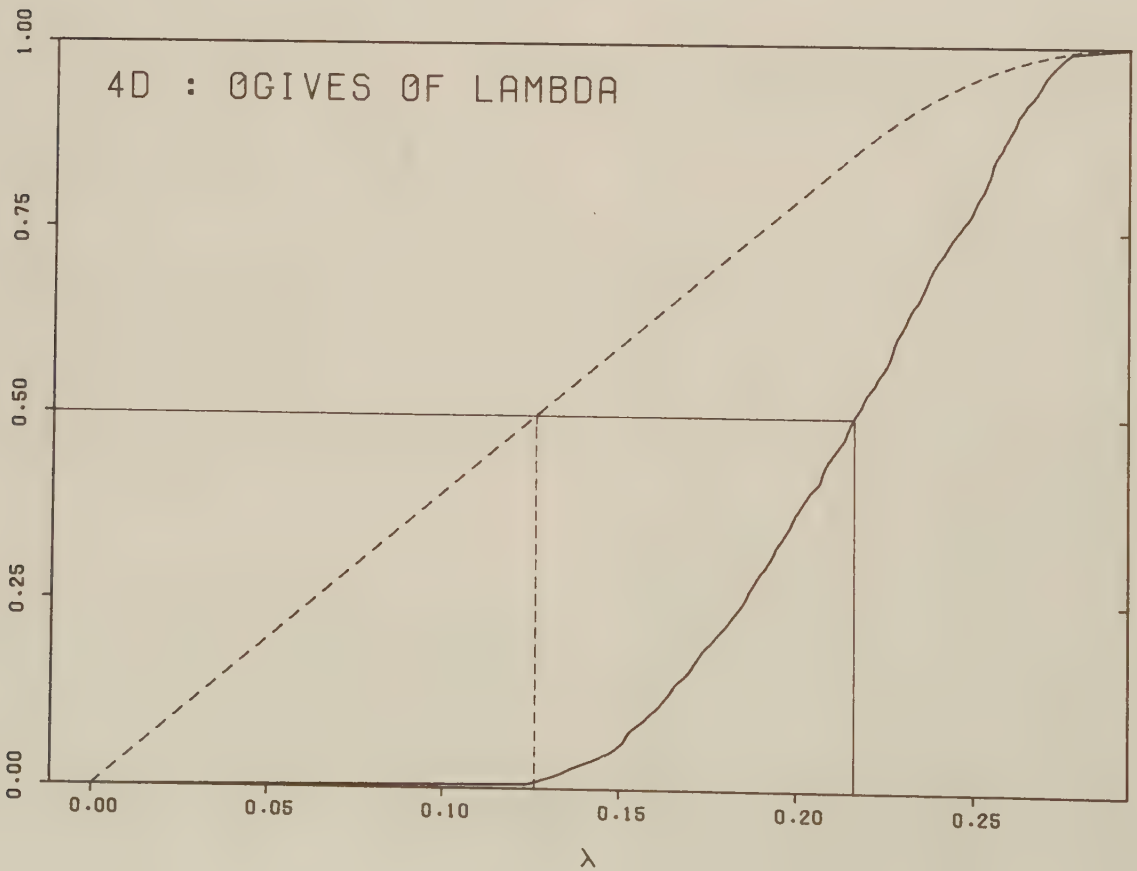

4D : 0GIVES 0F LAMBDA
1.00
0.75
0.50
0.25
0.00
0.00
0.05
0.10
0.15
0.20
0.25
λ

Table 6—Means of the probability distributions for the parameters of the population dynamics model, both for distributions initially constructed and for refinements incorporating the constraint of equation (15). Parenthesized figures are standard deviations followed by coefficients of variation. Note that R is expressed as a percentage. (See Appendix B for an explanation of the column headings under "Refined distribution".)

Parameter	Initial distribution	Refined distribution		
		Standard approach	Incorporating R/F correlation	Alternative to uniform assumption in initial distributions
R	3.90 (1.08 /0.277)	3.65 (1.03 /0.283)	3.68 (1.04 /0.283)	3.81 (1.07 /0.282)
F	0.394 (0.057/0.145)	0.371 (0.053/0.142)	0.372 (0.053/0.142)	0.378 (0.066/0.176)
S_a	0.825 (0.072/0.087)	0.917 (0.022/0.024)	0.917 (0.022/0.024)	0.921 (0.025/0.027)
M	0.197 (0.088/0.448)	0.087 (0.023/0.268)	0.087 (0.023/0.267)	0.083 (0.027/0.325)
λ	0.128 (0.075/0.586)	0.213 (0.038/0.180)	0.214 (0.038/0.178)	0.213 (0.045/0.213)
$s_2/s_3/s_4$	0.713 (0.185/0.260)	0.861 (0.058/0.068)	0.862 (0.058/0.067)	0.859 (0.069/0.081)

parameters that are functions of R, F, S_a, and λ: for example, sustainable harvesting rates.

Table 6 shows the means and standard deviations of the various parameters derived from their initial and refined probability distributions. (The latter are listed under "standard approach" in Table 6.) The distribution for juvenile survival rates $s_2/s_3/s_4$ was derived assuming constant (and maximal) values for ρ and q_f (cf equation (17)):

$$s_2/s_3/s_4 = \left[\frac{\lambda}{0.8 \times 0.45 \times S_a} \right]^{1/3} \qquad (18)$$

GENERAL DISCUSSION

Comparison of initial and refined estimates in Table 6 and Figure 4 shows, as might be expected, that imposing the constraint of equation (15) has the largest effect on the parameters whose initial estimates have the greatest coefficients of variation. The R and F distributions are little changed, while the S_a and λ distributions narrow considerably (see Table 6, "Standard approach").

In situations (as pertained here) where no direct evidence is available on mortality rates, the technique used has the potential to demonstrate that initial intuitive "guestimates" may be incompatible with other data. For example in this case, the technique served to eliminate initial intuitive impressions that S_a and $s_2/s_3/s_4$ could not be greater than 90%. Clearly, however, there is a danger of subjectivity ("adjusting initial distributions to force the answer you wanted in the first place") creeping in if iterative use of the technique is taken too far.

The approach should be considered a means of highlighting the parameters which are poorly determined and to which management recommendations are most sensitive to assist in fixing priorities for further research. An example in this regard is shown in Appendix C. Intuitively an age-determination program for adult females to provide independent data for S_a (and narrow the bounds on the initial 0.7 to 0.95 uniform distribution assumption) would seem a clear priority. (This would seem a more practical possibility than attempting direct assessment of all the juvenile survival rates that contribute to λ.) The example of Appendix C, however, suggests that priorities may in fact depend quite critically on the particular management question being asked.

In principle the population dynamics of each colony could be modeled separately using this technique. However, while all the colonies combined represent a closed population, individual colonies may be subject to emigration or immigration so that equation (15) would not apply. Indeed the technique used showed the difficulty of accounting for a high growth rate (~4%) per annum in the presence of heavy pup harvesting rates (~37%). An age at first parturition lower than 4 years would ease this, but what evidence there is points in the opposite direction (Shaughnessy 1982).

If the major mainland colonies do in fact each represent closed populations with annual growth rates ≈10%, survival rates considerably greater than those deduced for the population as a whole (adults 0.92, juveniles 0.86) would be needed. (For the extreme case $S_a = s_2/s_3/s_4 = 1$, $F = 0.37$, $\lambda = 0.36$, equation (15) yields a maximum possible increase rate of 14.9% per annum.) First-year survival rates may be higher for mainland colonies because of less space limitation and pups less vulnerable to mortality through being washed away in storms, but this could be offset by predation by jackals, *Canis* spp., and brown hyenas, *Hyaena brunnea* (Shaughnessy 1979). Nevertheless, given the extreme to which survival rate parameters would have to be pushed to account for "closed" Atlas Bay and Kleinsee increase rates (Table 2; an annual growth rate of 10% requires $S_a = s_2/s_3/s_4 = 0.957$), it would seem likely that immigration has played a role. (There are large island colonies near Wolf and Atlas Bays though not near Kleinsee.)

Evaluations on the basis of equation (15) have implicitly assumed constant parameter values (i.e., in particular no density dependence) which was the basis for derivation of that equation from equation (11). The resultant linear model and parameter estimates may well reflect a reasonable assessment of the average situation over the period 1971-83. Though the simplest assumption for the purpose of population projections and management recommendations might be to use these same parameter values for future years, considerable care should be taken in making such an extrapolation.

A particular priority (to allow the introduction of density dependence into the model) is to obtain further data for better determination of whether and at what rate the overall annual percentage growth is changing. (The present best estimate suggests an increase, but the standard error for this estimate is very large.) Improvement in precision could best be achieved by conducting further assessments for the major mainland colonies, particularly Wolf Bay and Atlas Bay.

ACKNOWLEDGMENTS

Discussions with P. B. Best, C. W. Clark, A. M. Starfield, and W. Zucchini are gratefully acknowledged, as are comments received on an earlier draft of the paper from J. Cooke, C. Fowler, J. Harwood, A. Hiby, P. Rothery, T. Stewart, and A. Trites. Part of this work was financed by a grant from the Sea Fisheries Research Fund (South Africa); subsequent work was carried out as part of the Benguela Ecology Programme (CSIR, South Africa).

CITATIONS

RAND, R. W.
1956. The Cape fur seal *Arctocephalus pusillus* (Schreber): its general characteristics and moult. S. Afr. Div. Sea Fish. Invest. Rep. 21, 52 p.

SHAUGHNESSY, P. D.
1979. Cape (South African) fur seal. *In* Mammals in the seas, p. 37-40. FAO Fish. Ser. 5, vol. 2.
1982. The status of seals in South Africa and Namibia. *In* Mammals in the seas, p. 383-410. FAO Fish. Ser. 5, vol. 4.
1984. Historical population levels of seals and seabirds on islands off Southern Africa, with special reference to Seal Island, False Bay. S. Afr. Sea Fish. Inst. Invest. Rep. 127, 61 p.
In press a. Population size of the Cape fur seal *Arctocephalus pusillus*. 1. From aerial photography. S. Afr. Sea Fish. Inst. Invest. Rep.
In press b. Population size of the Cape fur seal *Arctocephalus pusillus*. 2. From tagging and recapturing. S. Afr. Sea Fish. Inst. Invest. Rep.

SMITH, T., and T. POLACHECK.
1981. Reexamination of the life table for northern fur seals with implications about population regulatory mechanisms. *In* Fowler, C. W., and T. D. Smith (eds.), Dynamics of large mammal populations, p. 99-120. John Wiley & Sons, N.Y.

APPENDIX A
Some Aspects of the Calculation Procedures Used to Obtain Colony Size and Increase Rate Estimates

1. Assumption of a constant relative bias factor B_m for each assessment method

In a number of cases, the size of a colony was assessed by more than one method in a particular year. This provides the opportunity for checking the appropriateness of assumptions that B_m is constant for each method, in the absence of additional suppositions about year-to-year colony growth.

The ratio of *AM*, *AI*, *HM*, and *HF* to *TR* assessments for these cases have been plotted against the *TR* assessments in Figures 5 a-d. Means and standard deviations for these sets of ratios are shown in Table 3 (under the heading "Comparative Assessments").

The plots do not indicate any obvious trends. There is some suggestion of different patterns in the case of *TR* assessments <2000, where the *HF*/*TR* ratios are generally lower and the *AI*/*TR* ratios higher than average. (In the latter respect, four of the five data points refer to 1978 assessments of the closely grouped small island colonies off Luderitz: Marshall Reef, Staple Rock, Boat Bay Rock, and Dumfudgeon Rock.)

The average coefficient of variation for the tag-recapture assessments implies coefficients of variation for the associated ratios of 20%; other effects would increase this. Such large variation coupled with the smallish number of data points renders detection of any significant trend problematic. The assumption of constant B_m values does not appear, therefore, to be inconsistent with the data.

2. Appropriateness of minimization criterion utilized

The appropriateness of the criterion (expression (5)) used to determine maximum likelihood estimates of the parameters rests on the assumption of equation (3) that the residuals (which reflect the relative errors in $N_{m,c}(t)$),

$$\varepsilon_{m,c}(t) = \ell n\, \overset{obs}{N}_{m,c}(t) - \ell n\, B_m - \ell n\, N_c(0) - r_c t \qquad \text{(A1)}$$

are normally distributed with constant variance σ^2 (homoscedastic). To check the assumption of homoscedasticity, the magnitudes of the residuals have been plotted against the logarithms of expected population sizes $\overset{exp}{N}_{m,c}(t)$ in Figure 6.

Any trend in such a plot could be distorted by the fact that there tend to be fewer data points for the smaller colonies, so that as an estimate of σ, the root mean square residual for those colonies would be more negatively biased than for the larger colonies. To adjust for this effect, the plot shows not the $|\varepsilon_{m,c}(t)|$, but rather residuals "adjusted-for-bias" $|\varepsilon^*_{m,c}(t)|$ defined by

$$\varepsilon^*_{m,c}(t) = \sqrt{\frac{n_c}{n_c - 2}}\ \varepsilon_{m,c}(t) \qquad \text{(A2)}$$

$\psi\eta\varepsilon\rho\varepsilon\ n_c$ is the number of estimates for colony c. Colonies with $n_c = 2$ were disregarded.

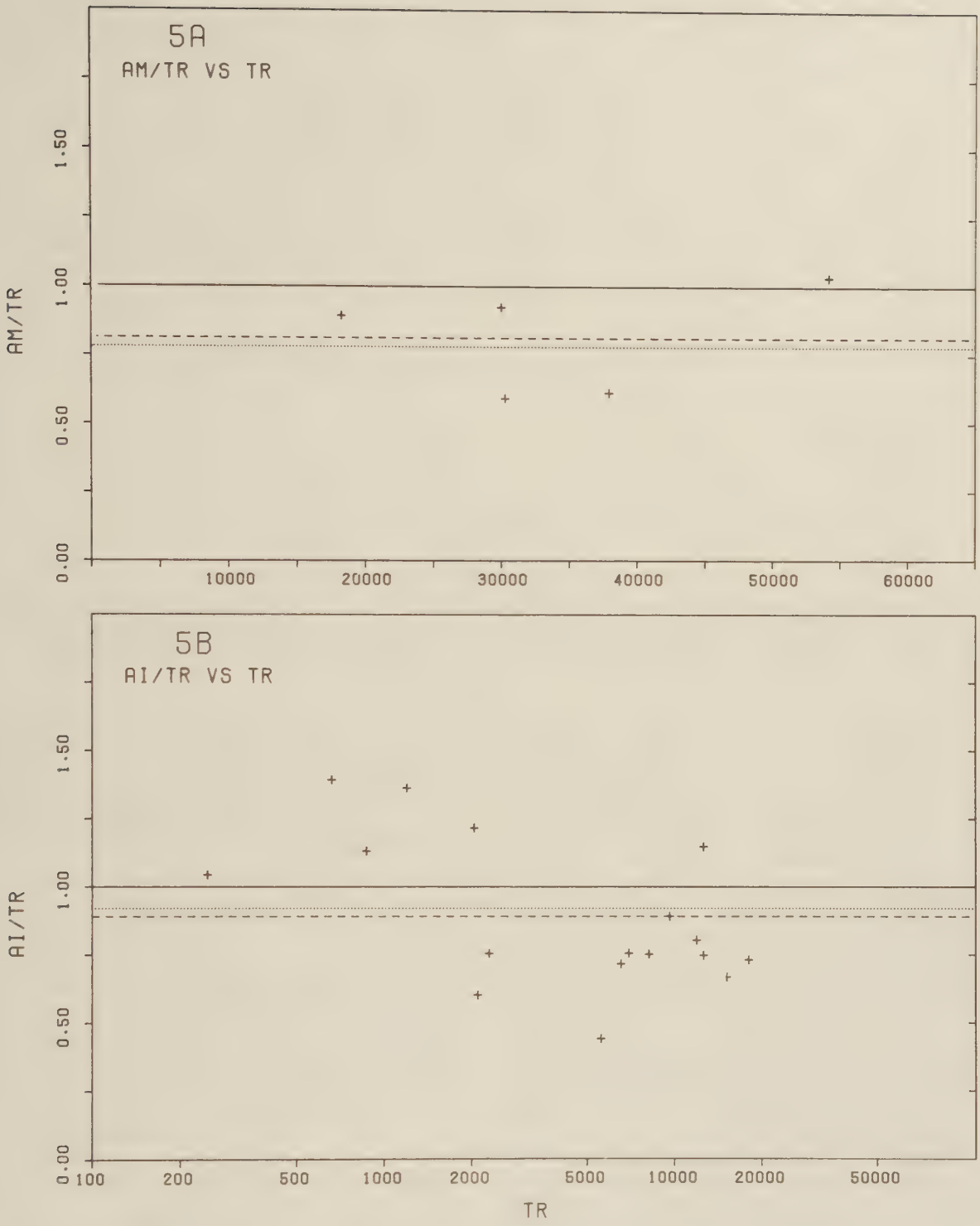
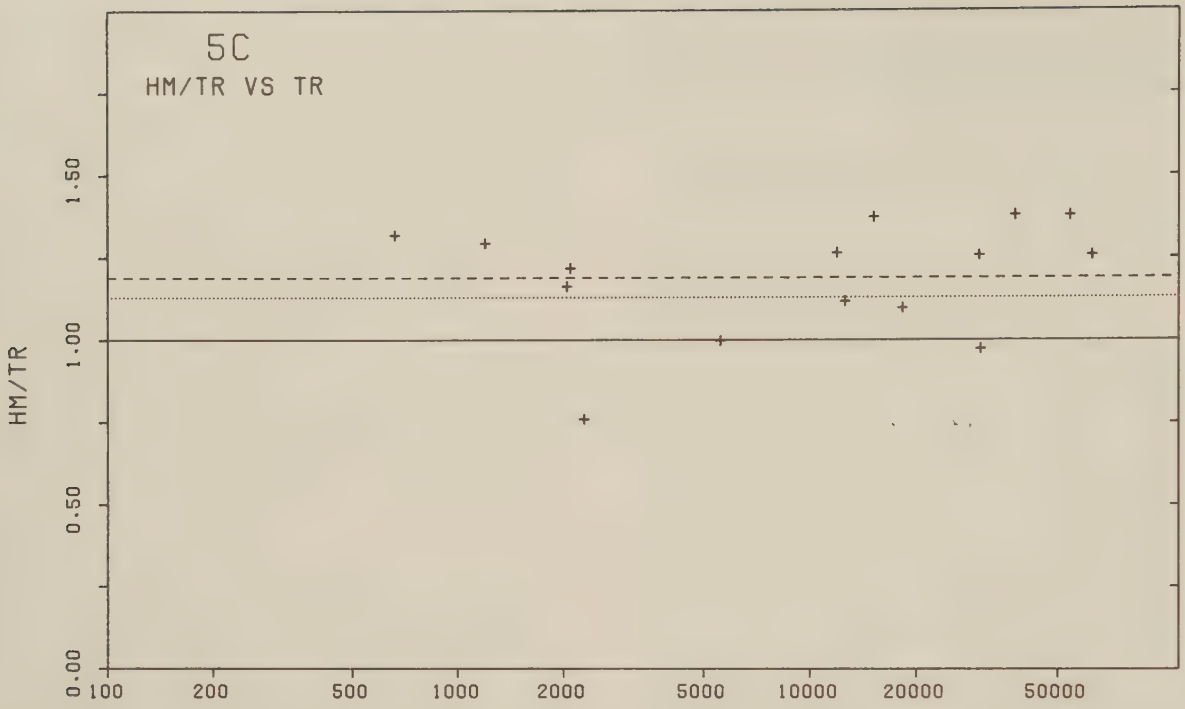
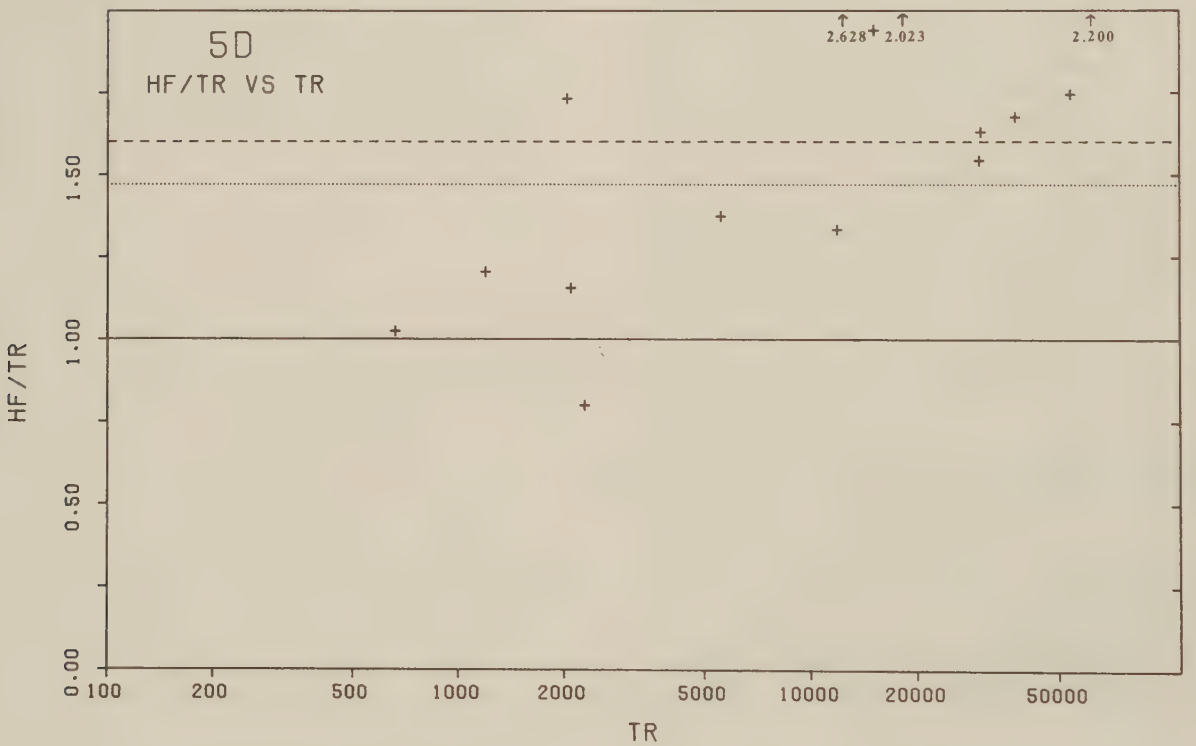


Figure 5—Ratios of comparative assessments (i.e., cases where a colony was assessed by more than one method in the same year) to the corresponding *TR* assessments. These ratios are shown (+) for (a) *AM*; (b) *AI*; (c) *HM* and (d) *HF* assessments, and are plotted against the value of the *TR* assessment. The mean ratio in each case is shown by a horizontal dashed line, and the corresponding B_m value estimated by the model fitting procedure (see equation (2); Table 3) by a horizontal dotted line. Note that the horizontal axis is log transformed for (b), (c), and (d).


5C
HM/TR VS TR
HM/TR
1.50
1.00
0.50
0.00
100
200
500
1000
2000
5000
10000
20000
50000


5D
HF/TR VS TR
2.628
2.023
2.200
HF/TR
1.50
1.00
0.50
0.00
100
200
500
1000
2000
5000
10000
20000
50000
TR

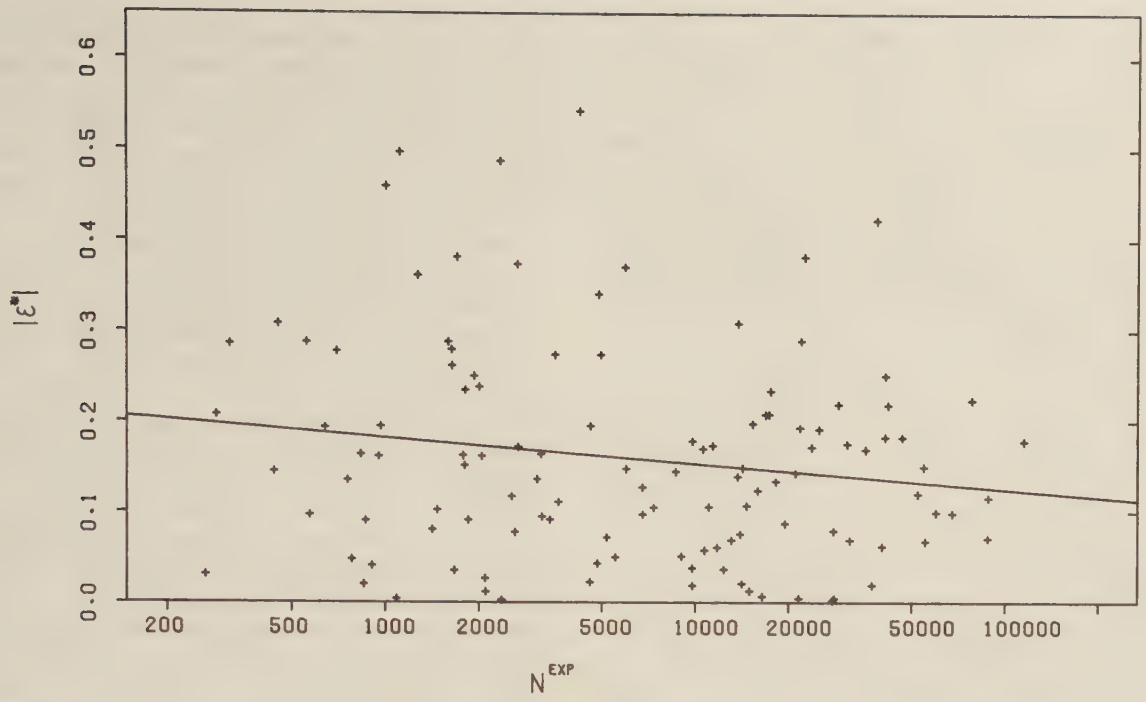


Figure 6—Values of residuals corrected for bias $|\varepsilon^*_{m,c}(t)|$ (see equation (A2)) plotted against expected colony pup population sizes $N^{exp}_{m,c}(t)$. The plot omits data for colonies for which only two assessments have been made, and for Black Rocks Algoa Bay. The horizontal axis is log transformed; the solid line is a linear regression fit to the data (similarly transformed).

To test for homoscedasticity, a linear regression fit of $|\varepsilon^*_{m,c}(t)|$ to $\ell n\ N^{exp}_{m,c}(t)$ was calculated and is shown in Figure 6. The (negative) slope is not significant ($P = 0.08$), however, so that the assumption of homoscedasticity is not contradicted.

The standard deviation of the residuals was estimated from

$$\sigma^2 = \frac{1}{n-(M+2C-1)} \sum_{m,c,t} [\varepsilon_{m,c}(t)]^2 \qquad \text{(A3)}$$

Inspection of a plot of the residuals $\varepsilon_{m,c}(t)$ indicated two of those for Black Rocks Algoa Bay were noticeable outliers. Indeed only for these points was $|\varepsilon| > 3\sigma$. Accordingly $\sigma^2$was recalculated omitting data from this colony. Such omissions are not relevant to estimates of the B_m parameters in the expression (5) minimization, as all assessments of this colony used the same method (*AI*). These outliers were also omitted in the homoscedasticity test detailed above. This calculation gives

$$\sigma = 0.232 \qquad \text{(A4)}$$

corresponding to a root mean square relative error in assessment of about 24%.

To see whether the overall results were sensitive to the estimated trend in mean error with colony size, the fitting procedure was repeated incorporating a weighting function into expression (5). This weighting function was taken to be the inverse of a linear regression fit to $[\varepsilon^*_{m,c}(t)]^2$ as a function of $\ell n\ N^{exp}_{m,c}(t)$; over the range of observed colony pup population sizes of some 200-100,000, it corresponds to a root mean square relative error decreasing from about 29% to 17%. Results are affected only marginally: for example, the average overall annual increase rate (R) estimate changes negligibly from 3.90 to 3.91%, with the associated standard error slightly reduced from 1.08 to 0.97%.

Use of the expression (5) criterion also assumes σ^2(method) (see equation 4) is constant. The average of the coefficients of variation for the assessments listed in Table 1 are *TR* 13%, *HM* 14%, and *HF* 15%. No such error estimates are available for the aerial assessments. Though these average values for the various tag-recapture procedures are virtually the same, values for individual assessments (excepting two large outliers for Dumfudgeon Rock) range from 5 to 25%. In principle these individual values could be incorporated in a weighting function introduced into expression (5); however, since this component accounts on average for only about one-third of the overall variation σ^2, and in the absence of standard error estimates for the aerial assessments, such additional sophistication does not appear warranted.

The root mean square relative differences between observed and expected population estimates (Table 1), excluding zeros and Black Rocks Algoa Bay, are as follows: *AM* 20%, *AI* 20%, *TR* 16%, *HM* 14%, and *HF* 24%. Superficially, this suggests that σ (method) for aerial assessments is greater than for tag-recapture procedures. However most *TR*/*HM*/*HF* assessments are linked triplets, and these results could be influenced by this. The larger value for *HF* compared to *TR* and particularly *HM* (reflected also in the standard deviation column for comparative assessments shown in Table 3) does indicate an additional contribution to the variation for this method. Conceivably this is caused by greater fluctuation in tagging mortality of the female pups, which are less robust and therefore may be more sensitive to differing handling procedures.

An advantage of the form of equation (3) is that the model becomes linear in its parameters upon log transformation, so that expression (5) can be minimized using matrix techniques. In this case, however, the computer program was structured for solution using a NAG minimization routine to allow investigation of error models corresponding to model transformations nonlinear in the model parameters.

3. Estimation of standard errors

Because the model used (equation (3)) is linear in its parameters upon log transformation, matrix techniques could also be used to provide standard error estimates for these parameters, and hence for population estimates and growth rates for individual colonies.

However, for subsequent analysis, error estimates (and likelihood functions) were required for population parameters for combinations of colonies. To avoid the complications and approximations of transformations and covariance contributions, the following Monte Carlo approach was adopted. Instead of the original set of "observed" assessments,

$$S = \{N^{\text{obs}}_{m,c}(t) : (m,c,t) = 1 \ldots\ldots n\}$$

a new set,

$$S' = \{N'_{m,c}(t) : (m,c,t) = 1 \ldots\ldots n\}$$

was generated where

$$N'_{m,c}(t) = N^{\text{exp}}_{m,c}(t)\, e^{\tilde{\varepsilon}} \quad \tilde{\varepsilon} \text{ from } N(0, \sigma^2)$$

$$= B_m\, N_c(0)\, e^{r_c t + \tilde{\varepsilon}} \qquad \text{(A5)}$$

using the values of B_m, $N_c(0)$ and r_c obtained from the expression (5) minimization, and of σ from (A3/A4) above.

Minimizing the expression

$$\sum_{m,c,t} [\ell n\, N'_{m,c}(t) - \ell n\, B_m - \ell n\, N_c(0) - r_c t]^2 \qquad \text{(A6)}$$

then yielded another set of parameter estimates B'_m, $N'_c(0)$, r'_c.

Repeating this process, a larger number (K) of times (calculations in this case used $K = 400$), yields a set of values of parameter α (where α could be any one of B_m, $N_c(0)$, r_c or any combination of these):

$$T : \{\alpha_k : k = 1 \ldots\ldots K\} \qquad \text{(A7)}$$

The standard deviation of the α_k's then provides the standard error estimate required. Confidence intervals (P values) quoted in the paper have also been evaluated on this basis.

The procedure, and also that used to estimate σ (A3), assumes that the $\varepsilon_{m,c}(t)$ are uncorrelated. This cannot be precisely true: *TR*/*HF*/*HM* procedures for a particular colony in a particular year cannot be completely independent.

For tag-recapture assessments, the average σ^2 (method) contributes only about one-third of the total σ^2, so that σ^2 (model) (see equation 4) is not insubstantial. Two of the effects that contribute to σ^2 (model) are deviations of the underlying colony growth trend from the exponential form assumed (equation (1)), and environmental effects (e.g., storms washing pups off islands causing variability in juvenile mortality).

Such environmental factors could introduce serial correlation effects. Different assessments for the same colony in a given year would be expected to be correlated in this manner, and nearby colonies might be affected similarly by the same environmental conditions.

There are some indications that such effects may be playing a role. If there were no correlation, one would expect the coefficients of variation for the ratios of comparative assessments (Table 3, rightmost column) to be approximately $\sqrt{2}\,\sigma = 0.328$. While the actual values for *AM*, *AI*, and *HF* are only slightly less than this, the value for *HM* is significantly smaller (*F*-test: $P < 0.005$), so that paired *TR* and *HM* assessments cannot be regarded as completely independent observations. Similarly the "anomalous" *AI*/*TR* ratios for the four Luderitz Bay islands referred to in Section 1 above are suggestive of intercolony correlations. Such correlations would bias both the estimation of σ (A3), and the Monte Carlo procedure for generating "alternative" assessments (A5).

Table 7 shows a matrix of the signs of discrepancies between actual and model predicted assessments for all data used in the parameter estimation procedure. The only significant feature is the predominance of positive discrepancies for all methods in 1977 ($P = 0.02$). Otherwise there are no obvious patterns.

Considering colony-years where both *TR* and *HM* assessments took place, the frequency of (double positive:opposite sign:double negative) discrepancies is (4:6:5). Similarly, for *TR*/*HM*/*HF* triplets the frequency is (3:4:6:2). Neither case reflects significant difference (χ^2 test: $P = 0.69$ and $P = 0.63$ respectively) from the expectation in the absence of serial correlation effects (though for small data sets, the model-fitting procedure could bias such a test).

If the *HM* values (16 in all) are omitted from the calculations because of indications of correlations between *TR* and *HM* assessments, the standard error of the overall average annual increase rate (R) increases from 1.08 to 1.40%. This is a larger increase than might naively be expected from the reduction in number of degrees of freedom in the fitting process (82 → 67). However, a disproportionate number of the *HM* assessments relate to the large mainland colonies which dominate in the calculation of R. More significantly perhaps, the estimate of σ increases to 0.245 (i.e., 6% larger, albeit not statistically significantly so), which may be indicative of the order of magnitude of serial correlation effects in the standard error calculations.

Thus, though serial correlation effects would be expected and there are some indications of their existence, there appears no obvious evidence that they are sufficiently marked to bias standard error estimates grossly. Given the paucity of data, elaboration of the error model to attempt to quantify such effects does not seem warranted, and the assumption of absence of serial correlation in calculating standard errors appears a reasonable first step to take.

Table 7—Signs of the discrepancies between actual and model predicted (equation (2)) assessments at the various breeding colonies for data used in the parameter estimation procedure. To distinguish assessment methods, the notation *AM* (or *AI*)/*TR*/*HM*/*HF* is adopted; blanks indicate absence of such assessment, with trailing /'s omitted. Zeros indicate situations with only two assessments for the colony, and so an exact model fit.

Colony		1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983
Cape Cross			−					+			−/−/−/+			
Wolf Bay					/ /+/−					−/+/−/+				
Atlas Bay					−/+/+/+			−		+/−/+/+				
Kleinsee			+	+/−/−/−				+			+	/−/−/+		
Van Reenen Bay			0								0			
Lions Head			0					0						
Marshall Reef			−					+	−/−					
Staple Rock			−					+	+/−/+/+		−			
Boat Bay Rock			−					+	+/−		−			
Dumfudgeon Rock			+					−	+/−/+/−		+			
Long Islands			−					−/+/+/+			−			−/+
Albatross Rock			+					−/+/+/+			−			−/+
Sinclair Island			+					−	−/−/+/−		+			−/+
Elephant Rock			+				+/−/−/−	+			+			
Robbesteen			−					+			−			
Seal Island FB		+/−/−/+						+			−		−/−	+
Geyser Rock			−				+/+	+			−		−/+	
Quoin Rock			+			+/+/−/−		+			+			
Seal Island MB			−			−/+/+/−		+			−			
Hollams Bird Is			0					0						
Black Rock								0			0			
Jacobs Reef			0					0						
Black Rocks AB			+					−			+			
Aerial	+	1	7	1	0	1	2	11	3	1	6	0	0	1
Methods	−	0	8	0	1	1	0	6	2	1	9	0	2	3
All	+	2	7	1	4	4	3	17	7	5	7	1	1	4
Methods	−	2	8	3	2	4	3	6	9	3	11	2	3	3

APPENDIX B
Some Aspects of the Approach Used to Refine Parameter Distributions

The approach consists of replacing the initially constructed 4-dimensional joint probability distribution for parameters R, F, S_a, and λ by a "refined" distribution which is proportional to the intersection of the initial joint distribution with the hyperplane defined by the constraint of equation (15).

This is an ad hoc procedure, which seeks to update the initial distributions on a basis which in some sense maximizes their mutual consistency with the equation (15) constraint. By construction it has the desired effect of generally according more weight to parameters whose probability distributions have smaller coefficients of variation (i.e., for which there is better information) in the refinement process.

In this case analytic generation of the intersection required is impractical, while numeric generation according to the appropriate initial probability distributions (by use of random numbers) of $\{R, F, S_a, \lambda\}$ sets satisfying equation (15) within some tolerance would be a lengthy procedure. However, the latter procedure is in the limit of vanishing tolerance exactly equivalent (J. Cooke, Dep. Biol., Univ. York; T. Stewart, Dep. Math. Stat., Univ.Cape Town, pers. commun.) to generating values for any three of the parameters in this manner, evaluating the fourth using equation (15), and then according the resultant set of four values a weight given by the initial probability distribution of that fourth parameter.

Though in principle any of the parameters could be chosen as the "fourth" in this context (the approach treats the parameters equivalently in this sense), it was computationally simplest to take λ as that parameter. Thus R, S_a, and F values were generated and λ then calculated using equation (15). If $0 \leqslant \lambda \leqslant \lambda_{max}$, the set of four values was given unit weight, otherwise discarded (see equation (17) and following; the λ distribution was assumed uniform over 0 to λ_{max}). About 25% of the sets thus generated were retained, so that the process of producing 10,000 sets was computationally very rapid. Results are shown in Table 6 under the heading "Standard approach".

By construction the initial probability distributions for S_a, λ, and F were not independent, as components of both λ and F were functions of the value of S_a. The actual correlation is fairly weak ($|r| < 0.2$); however, the refinement process imposes a different correlation structure on the joint distribution, with R and λ ($r = +0.37$) and particularly λ and S_a ($r = -0.69$) showing strong correlation as might be expected. These covariances can influence evaluations of standard errors of functions of the parameters, such as sustainable harvesting rates, quite considerably.

The standard approach has treated the initial R and F probability distributions as independent. This is not strictly true, as there is a significant (albeit small, $r = +0.16$) correlation between R and N_{TR}^{exp}, the latter of these contributing to F. The refinement approach can still be applied in this case, though the random number generation procedure becomes discrete in selecting one of the (R, N_{TR}^{exp}) pairs produced by colony size calculation procedures (expression (A6) and following), rather than continuous in linearly interpolating over an ordered set of estimates for a single parameter. The results of this are shown in the column "Incorporating R/F correlation" in Table 6; their differences from the standard approach are minimal.

An important consideration is the sensitivity of the refined distributions to assumptions made in constructing the initial distributions, the most "arbitrary" aspect of which was the uniform distributions assumed for μ (bias of TR estimate), s_{11} (survival rate of pups from tagging to harvest), S_a, and λ. The extremities of these distributions are considered to have been conservatively chosen (i.e., ranges as wide as conceivable) so that the principal concern is the assumption of distribution uniformity.

For the parameter range a to b, a uniform distribution corresponds to assuming equal length intervals within the range are equally likely (to contain the actual parameter value). Why should this be appropriate for the parameter chosen rather than some transformation thereof (e.g., uniformity for S_a does not correspond to uniformity for $M_a = -\ell n\, S_a$)? Serious bias in the results of the refinement procedure is most likely if successively smaller intervals are equally likely as the extremities of the range are approached, i.e., if the initial distribution for the parameter chosen is U-shaped rather than uniform.

Accordingly, the overall procedure was repeated with all uniform initial probability distributions over their respective ranges a to b replaced by a probability density function $f(x)$ which is a fairly extreme example of such a U-shape:

$$f(x) \begin{cases} = 0 & x < a \\ \alpha\ [(x-a)\ (b-x)]^{-1/2} & a \leqslant x \leqslant b \\ = 0 & x > b \end{cases} \qquad \text{(A8)}$$

This integrates conveniently to yield

$$\text{Prob}\ (X < y) \begin{cases} 0 & y < a \\ \dfrac{2}{\pi} \arcsin \sqrt{\left(\dfrac{y-a}{b-a}\right)} & a \leqslant y \leqslant b \\ 1 & y > b \end{cases} \qquad \text{(A9)}$$

and is readily incorporated in the computational procedure.

The results are shown in the final column of Table 6 under the heading "Alternative to uniform assumption in initial distributions". The coefficients of variation for the refined F, S_a, and λ are slightly larger ($\sim$20% increase) compared with the standard approach as might be expected, but otherwise differences are very small.

The result of the exercise of Appendix C is also relatively insensitive to this modification of procedure. The value for C^a (see equation (A13) and following) changes from 15,100 to 15,600, and the associated standard error from 5,100 to 5,470.

APPENDIX C
An Example of Use of the Parameter Distribution Refinement Approach to Determine Parameters To Which Management Recommendations Are Most Sensitive

Consider the question: What average annual harvest of females past the age of first parturition over the period 1971-83 (in addition to the pup harvest that was taken) would have kept the overall population size constant? It is assumed that such females had been harvested at the same time as the pups (7 months into the year), and that the survival of a pup whose mother was removed at that time would not have been impaired.

If C_t^a is the number of such females harvested in year t, then the first term on the right hand side of equation (11) is adapted as follows:

$$\eta_t S_a \rightarrow (\eta_t S_a^{7/12} - C_t^a) S_a^{5/12} \qquad \text{(A10)}$$

and equation (15) then becomes

$$(1 + R)^4 = (1 + R)^3 S_a (1 - F^a) + \lambda(1 - F) \qquad \text{(A11)}$$

where $F^a = \dfrac{C^a}{\eta S_a^{7/12}}$

For a constant overall population, $R = 0$, so that equation (20) yields

$$F^a = 1 - \frac{1 - \lambda(1-F)}{S_a} \qquad \text{(A12)}$$

Using the relation (see equation (16) and following)

$$\mu N_{TR}^{\text{est}} = \eta \rho s_{10}$$

the appropriate average female harvest level is then calculated as

$$C^a = F^a \eta S_a^{7/12}$$

$$= \left\{1 - \frac{1 - \lambda(1-F)}{S_a}\right\} \frac{S_a^{7/12} \mu}{\rho s_{10}} N_{TR}^{\text{est}} \qquad \text{(A13)}$$

Taking maximal values for ρ and s_{10} of 0.8 and 1, respectively, yields the (thereby negatively biased) result:

$$C^a = 15{,}100 \text{ (SE } 5{,}110).$$

(Note: For the number of data sets generated, results are essentially correct to three significant figures and so have been rounded accordingly.)

To what extent would better information on adult (female) survival rates S_a improve the accuracy and precision of this estimate? Assume independent methods provided a normal probability distribution for the adult natural mortality rate with a certain mean and coefficient of variation. Table 8 shows the results of using such information rather than the probability distribution constructed in the previous section for S_a, for a wide range of values for the mean and coefficient of variation. Interestingly, neither is the result particularly sensitive to the estimate of S_a, nor is its standard error much affected by the precision with which S_a is estimated. For mean M_a values between 0.06 and 0.12, means for the C^a distributions differ only by a maximal ~7%, while coefficients of variation are all ~33%.

Accordingly, from the point of view of answering the question posed, this analysis indicates that field determination of the pregnancy rate (ρ) and pup survival rate between birth and tagging (s_{10}; conceivably by a series of aerial surveys over this period) would warrant higher priority than obtaining data on the adult female age distribution (to estimate S_a). This is because the answer required, while insensitive to S_a, is inversely proportional to both ρ and s_{10} which were both assumed fixed at maximal values for the calculations, and could in reality be markedly less than those maxima.

Table 8—Estimates of C^a, the number of female seals past the age of first parturition that would need to have been harvested annually to maintain the total population at a constant level over the period 1971-83.[a] Estimates are given on the assumption that a normal probability distribution is available for an estimate of the adult natural mortality rate M_a, and results are shown for various combinations of means and coefficients of variation for such a distribution. The central value for mean M_a = 0.087 corresponds to the value obtained by the "Standard approach" (Table 6). Parenthesized figures are standard errors followed by coefficients of variation. All results have been rounded to three significant figures.

Mean M_a (yr^{-1})	0.03	0.06	0.087	0.12	0.15
$S_a = e^{-M_a}$	0.970	0.942	0.917	0.887	0.861
Coefficient of variation for M_a					
0.01	13600 (4510/0.332)	14800 (4910/0.333)	15700 (5190/0.331)	15200 (4960/0.327)	11100 (3670/0.330)
0.05	13600 (4620/0.339)	14800 (4960/0.335)	15600 (5160/0.331)	15200 (5010/0.329)	12000 (4110/0.342)
0.10	13600 (4600/0.338)	14800 (4960/0.335)	15600 (5240/0.336)	15200 (5060/0.333)	13500 (4710/0.348)
0.20	13600 (4640/0.341)	14800 (4950/0.335)	15300 (5100/0.333)	15300 (5100/0.334)	14900 (5100/0.344)
0.30	13500 (4590/0.340)	14800 (4990/0.338)	15200 (5080/0.333)	15200 (5120/0.338)	15000 (5080/0.338)
0.40	13700 (4680/0.342)	14600 (4970/0.340)	15000 (5080/0.338)	15000 (5050/0.337)	15000 (5070/0.338)

[a]Note: It can be shown that $F^a \approx R(F^a = 0)\left[\dfrac{4}{S_a} - 3\right]$ so that the comparative insensitivity of C^a to S_a, and in particular the eventual decrease of C^a as S_a decreases may seem surprising. The underlying reason is that as S_a is decreased, the constraint equation (15) mitigates against high R values, so that mean of the refined probability distribution for R eventually decreases too.

[Note: Results of these calculations are presented as the value of a harvest C^a rather than a harvesting rate F^a, as any practical management decision would need to be in terms of the former, and so take into account uncertainties in additional factors required to estimate C^a given F^a. For simplicity, the analysis that the harvesting rates (F and F^a) were constant over the 1971-83 period, and provided an unbiased estimate of F^a in this context. (This value of 5.5% (SE 1.6%) is, like C^a, relatively insensitive to the mean and coefficient of variation of the initial probability distribution for M^a.) However, F and F^a relate to harvests C and C^a through the number of reproducing females η. Imposing F^a is intended (in terms of the original question posed) to keep at its 1971 level, which is lower than the average 1971-83 value used in the calculations above. Further, for C fixed, this lower η would lead to a higher F value than that for the case $F^a = 0$ (as assumed above). More detailed calculations could eliminate this element of positive bias in C^a estimates quoted, but would not, however, affect the validity of the conclusion above on relative sensitivity of the result to different parameters.]

Ecology, Behavior, and Survival of the South American Fur Seal in Uruguay

RAUL VAZ-FERREIRA
Departamento de Zoologia de Vertebrados
Facultad de Humanidades y Ciencias
Tristan Narvaja 1674
Montevideo, Uruguay

ABSTRACT

South American fur seals, *Arctocephalus australis*, in Uruguay were not driven as close to extinction by early sealers as other fur seals. The herd probably never numbered less than 3,000 pups per year (5,000 adults minimum). The ecological and behavioral traits that may have contributed to the species in Uruguay being somewhat buffered against the effects of sealing are compared here with other species. These traits were: (1) sealing occurred in winter when breeding seals are mostly at sea; 2) the groups exploited were mostly males; 3) these seals prefer steep, rocky terrain that hampered sealers and allowed many seals to escape harvests; 4) these individuals are shy and flee from humans; 5) displaced or undersized individuals will breed if a reduction in adults occurs; 6) seals spend long periods of time at sea in response to disturbance. These traits are contrasted with fur seal species that were affected much more profoundly by sealing activities.

INTRODUCTION

The Uruguayan herd of South American fur seals, *Arctocephalus australis*, has survived 400 years of exploitation, during which time it has probably gone through many unrecorded and a few recorded important changes in population size. The total number of pups born annually has certainly been above 3,000, which means a minimum of 5,000 adults. This contrasts with the historic minimums reached by other species of fur seals. For example, the minimum population reached by *A. phillippi* was around 450 (D. Torres - Navarro, Inst. Antarct. Chileno, Santiago, pers. commun.), less than 100 to a few hundred for *A. galapagoensis* (OEA 1978) and *A. townsendi* (Kenyon 1973), and about 100 for *A. gazella* (Bonner 1976).

The goals of this paper are to describe ecological and behavioral adaptations of *A. australis* that may have helped buffer the species against the effects of past sealing, and that may help explain the current population trends. These adaptations will be contrasted with those of species that were once on the verge of extinction.

The main positive and negative factors for the survival of the fur seals in Uruguay appear to be connected with the land habitat. The breeding habitat comprises parts of six islands and islets between 34°24′S, 53°45′W, and 35°01′S, long. 54°52′W. In addition to these breeding islands, which are populated year-round, small hauling grounds are present during the breeding season at Cabo Polonio, Islote de Coronilla, and exceptionally on Isla Gorriti. All of these islands have mixed topography in which rough and smooth terrain vary in different proportions. They vary in size from 41 ha (Isla de Lobos) to less than 1 ha (Islote de Torres). Water temperatures at these islands vary from 11° to 14°C in winter and from 18° to 25°C in summer.

RESULTS

Changes in population size

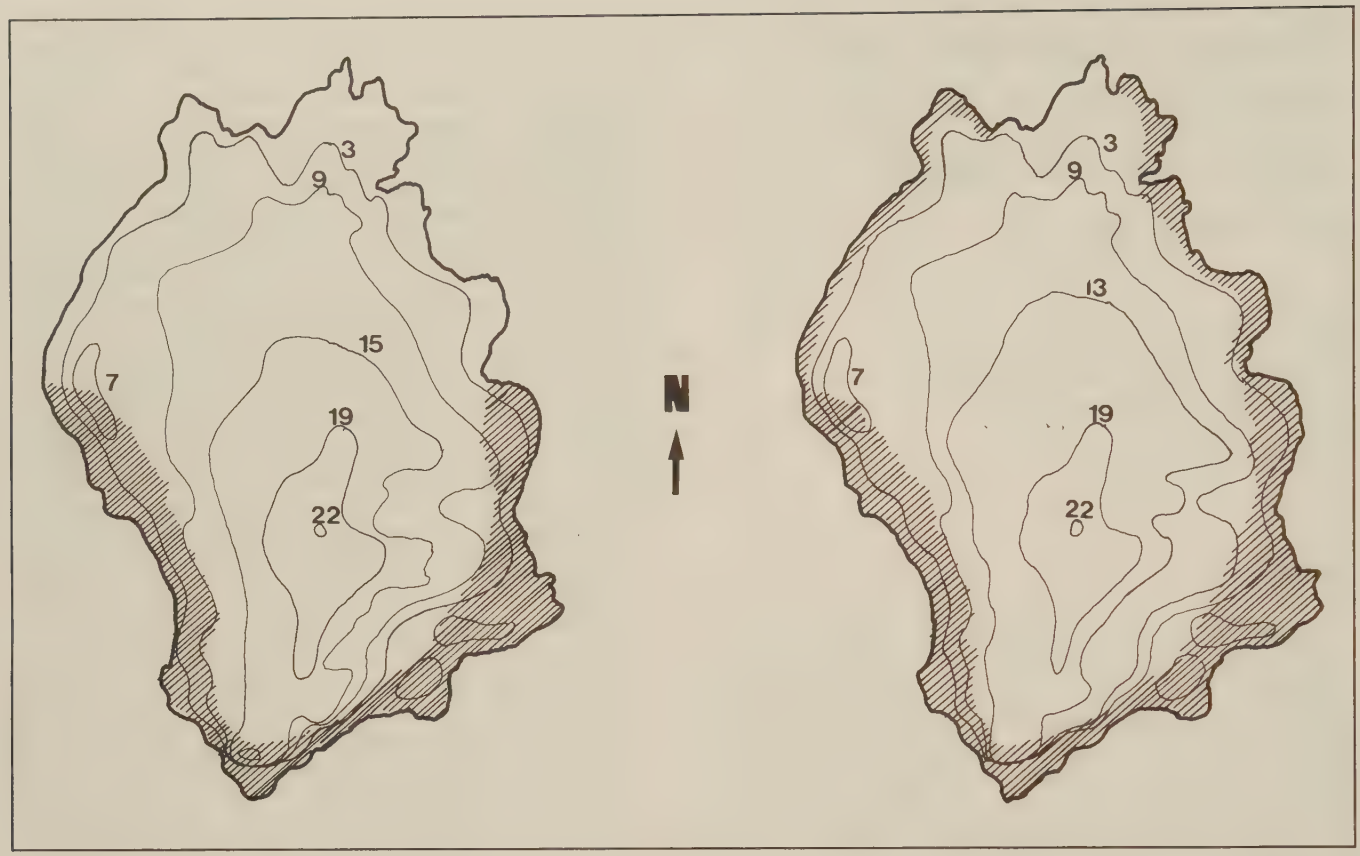
An increase of *A. australis* in Uruguay is suggested by counts and by the kill for pelts (annual average from 1968 to 1981: 11,036). A complete count of fur seals on all islands during the 1953 breeding season totaled 26,444, including 9,149 pups (Vaz-Ferreira 1982). No attempt was made to estimate the total herd size (including seals at sea).

A few comparative pup counts exist for Isla de Lobos and Isla Rasa (Table 1). These counts were made in February when pups were 2 or 3 months old and had experienced variable mortality (usually 10 to 20%, Vaz-Ferreira et al. 1985). The comparison of 1956 and 1981 shows an increase of 99%.

Table 1—Pup censuses for two colonies of South American fur seals.

	Number of pups counted	
Year	Isla de Lobos	Isla Rasa
1953	4,435	15
1956	7,460	178
1981	14,815	—
1984	—	5,000*

*Minimum number.



Figures 1-2—Areas occupied by breeding grounds and pups on Isla de Lobos in 1956 (left) and 1981 (right). Heights are given in meters.

On Isla de Lobos most of the increase in population in 1981 occurred either on flat or noncliff areas which had no pups in the 1956 counts. These are the lower, more unprotected (from high surf) parts of the islands. Pup mortality in these areas is usually greater than on the more protected parts of the islands, due to storms. At low densities, mortality on low areas was rare. The increasing area occupied by breeding grounds and pups is shown in Figures 1 and 2 (Isla de Lobos) and Figures 3 and 4 (Isla Rasa).

Annual cycles—Some areas are populated year-round, while others are occupied only seasonally. On areas that are used all year, males are always territorial to some degree, and females use the breeding areas to suckle their young.

In winter some islands of relatively small diameter, such as Isla Rasa and Islote de Lobos, may be completely covered by seals. In summer, the area with compact herds may extend 10 to 50 m into the islands, although this area changes with temperature and surf conditions.

Land-use patterns in winter are more variable than in summer. For example, from 1956 to 1981 the number of seals in winter on the higher parts of Isla de Lobos underwent a progressive reduction. Some of this variation may have resulted from weather conditions, some may have been long-term behavioral reactions to repeated sealing, and some may have been responses to increased commercial fisheries.

Very little is known about the problems this species faces in its marine habitat, except that mortality at sea in young individuals is small compared with species that either perform regular migrations or spend longer annual periods at sea. Reduction of sea time diminishes exposure to marine predators. Nevertheless, adults are exposed to some predation by sharks and killer whales during feeding trips which may extend more than 220 km from shore to 200 m depth.

The species does not habitually feed near shore, nor in fishing nets; therefore it is not killed by fishermen as are South American sea lions and South African fur seals. However, some young animals drown in trammel nets set too near breeding areas.

Sealing—*A. australis* in Uruguay may never have been reduced to excessively low numbers partly because exploitation has been based on common sense or technical criteria for more than 100 years (Vaz-Ferreira 1976a,b, 1980, 1982). The success of this approach is apparent from the herd's increase. For many years killing was indiscriminate with little limitation of the catch. In many years 8-month-old pups were included in the kill because they met market size requirements. In 1950, killing was restricted exclusively to males. Individuals in the corrals were captured and sexed to avoid killing females. This kind of selection was later changed when it was found that most of the animals on the highest parts of the islands were young males (Ximenez 1962). In 1980 killing was reduced and restricted to adult males because excessive pelts had been stockpiled.

For commercial and practical reasons, sealing now occurs from June or July to September or October, although before 1876 it occurred throughout the whole year. In winter and early spring most seals are on the upper (nonbreeding) parts of the islands. Massive attendance on land, on which the success of sealing depends, is not regular (Vaz-Ferreira 1975). In some years the capture of seals on the higher parts of islands failed to produce the expected harvest, and therefore sealers obtained additional seals from the shore

Figures 3-4—Areas occupied by breeding grounds and pups on Isla Rasa in 1956 (left) and 1984 (right).

(breeding) areas. These latter drives included a large number of females due to their permanent attendance on those areas. Therefore, drives made on higher parts are less damaging to the breeding population, at least in the short term, than drives on the shores of islands.

Terrain—The impact of sealing on the herd is altered by terrain. Unlike some other species of fur seals, *A. australis* prefers to breed on very rocky, inaccessible parts of islands. This is facilitated by some particular abilities, such as climbing. On entirely flat islands that can be completely surrounded by sealers, virtually the entire population can be taken. Even when many of the seals escape, repeated operations on flat islands cause the breeding population to decline almost to zero. This apparently happened on Isla Rasa in the 1950s.

Killing is most controlled on Isla de Lobos where seals are captured far from the sea and driven into corrals prior to killing. On rocky islands, like Torres and Castillos, killing is least selective because sealers must stop the running seals and kill them near the sea. On islands with mixed topography, the sealing operation is easier where seals are far from sea and where the terrain is more or less flat. Sometimes drives in such areas yield 4,000 seals. On the rough parts of these islands, which are much closer to sea, a higher percentage of seals escape to the water than from the high parts. On Isla de Lobos and Isla Marco, crevices and caves near the sea allow seals living on them to escape the sealers.

If big territorial males are shot during field experiments, smaller males, formerly excluded from the breeding areas, replace them in their activities within 24 hours (Vaz-Ferreira 1980).

Different populations of *A. australis* occur in Argentina, Chile, and Perú and nearby islands. Connections between them and the Uruguayan population have not been found. However, individuals tagged in Uruguay have been recovered in non-breeding areas as far away as Rio de Janeiro (Brazil) and Bahia Blanca (Argentina). In Uruguay, individuals 38 to 42 months old have been found on islands different from the natal ones, but there is no evidence of these individuals breeding in new areas. Six-month-old pups remain near their natal areas and resort always to the same islands on which they were born.

The increase of the populations on the Uruguayan islands observed from 1973 to 1981 was simultaneous on the different sites.

Microclimate—On some of the islands, particularly Isla de Lobos, rainwater pools, springs, or shady areas favor the establishment of pup groups and of small breeding groups (one to five territorial males with females and pups) as far as 200 m from the main breeding areas on the shores. Also, soil made wet by passing of animals returning from sea, by urine, and by wind-blown spray is suitable for individuals which stay there. However, these inland breeding areas are relatively few and contain not more than 2-5% of the territorial males.

The tidal excursion is small (about 1 m in summer). Some breeding grounds are wet at low tide. Many territorial males must hold position at high tide.

Changes in behavior—During the increase of the herd between 1948 and 1984, some changes were recorded in the ecology and behavior of seals. At low population levels the breeding areas were restricted to rocky areas, caves, or places near pools; that is, in a reduced part of the available space. In these areas the pups could escape to higher ground during high seas. No breeding occurred on flat, low areas, which were deserted, occupied by male groups, or occupied by sea lions.

The move onto low areas caused some new behavioral traits, such as resting on sand at high temperatures. Also, interindividual distance decreased in nonbreeding groups, and previously unrecorded contact behavior began to occur.

Outside the breeding season, when harvesting occurs, seals flee from humans that approach closer than 100 m. Adult females and juveniles flee at all seasons, and adult males flee except during the breeding season.

Responses to storms—In some years, storms in December and January are principal causes of pup mortality. During storms mothers do not have time to carry their pups to high ground. Many thousands of such pups, particularly in low areas, are either drowned or are driven to the mainland shore where they cannot be found by their mothers. About 3,000 pups were washed onto Cabo Polonio after a storm on December 30, 1979, from islands that are 600 to 3,000 m from the cape. Similar mortality was seen at Cabo Polonio in the breeding seasons of 1981-82, and 1982-83 (unpubl. data). Such storms probably affect more pups than those counted because many drowned pups never wash ashore. Since this type of mortality was either absent or very infrequent around 1956, it is probably a consequence of the increase of population on the nearby islands.

SUMMARY

The principal factors which favored the survival of the Uruguayan population of fur seals during the period of unregulated sealing were:

(1) Kills were made in winter when a large portion of the breeding individuals were at sea.

(2) The groups most accessible to sealers were on the higher parts of islands and were composed mostly of males (Ximenez 1962).

(3) The steep, rocky areas favored by seals for breeding and during the winter hampered access by sealers, and allowed many seals to escape harvests. With reduced exploitation, inaccessible populations produced seals that repopulated more accessible areas formerly hunted to extinction.

(4) During winter individuals are extremely shy, and will flee from humans that are closer than 100 m.

(5) Displaced or undersized individuals will breed if a reduction in adults occurs.

(6) Seals, especially nonbreeders, tend to remain at sea for long periods of time in response to disturbance, thus reducing the numbers available for exploitation.

These traits contrast with those of other *Arctocephalus* species that were once nearly extinct. For example, *A. townsendi*, although tending to inhabit caves, had an extreme innate tameness (Kenyon 1973). *A. gazella* bred in open, unprotected areas where the populations were very exposed to killing. Finally, *A. phillippi* bred in extensive, open colonies, yet a few managed to survive inside caves (Torres et al. 1979).

A least one mechanism regulates the *A. australis* population when it reaches high levels. Under crowded conditions, breeding groups and pups occupy low, unprotected areas of islands where storms and high seas often cause increased mortality of pups.

CITATIONS

BONNER, W. N.
1976. The status of the Antarctic fur seal *Arctocephalus gazella*. ACMRR/MM/SC/50. FAO, Sci. Cons. on Mar. Mamm., Bergen, Norway, 8 p.

KENYON, K. W.
1973. The Guadalupe fur seal (*Arctocephalus townsendi*). IUCN Publ. N.S. suppl. pap. (39):82-87.

OEA.
1978. Meeting of experts on conservation of marine mammals and their ecosystems, Puerto Madryn, Chubut, Argentina, 1977. OEA/Ser. J/XI, CICYT/doc. 183:1-59.

TORRES, D. N., V. YANEZ, J. CATTAN, and P. E. CATTAN.
1979. Mamiferos marinos de Chile: antecedentes y situacion actual. Biol. Pesq. Chile 11:49-81.

VAZ-FERREIRA, R.
1975. Factors affecting numbers of sea lions and fur seals on the Uruguayan Islands. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 169:257-262.
1976a. *Arctocephalus australis* (Zimmermann) South American fur seal. ACMRR/MM/SC/49. FAO, Sci. Cons. Mar. Mamm., Bergen, Norway, 13 p.
1976b. *Arctocephalus australis* (Zimmermann). South American fur seal Addendum. ACMRR/MM/SC/Add. 1. FAO, Sci. Cons. Mar. Mamm., Bergen, Norway, 3 p.
1980. Aspectos eto-ecologicos, explotacion y conservación de algunos Otariidos. I Reun. Iberoam. Zool. Vert., La Rabida, Espana, 7:263-282.
1982. *Arctocephalus australis*. Zimmermann, South American fur seal. *In* Mammals in the seas, p. 497-507. FAO Fish. Ser. 5, vol. 4.

VAZ-FERREIRA, R., E. LESSA, F. ACHAVAL, and A. MELGAREJO.
1985. Recuento de cachorros de lobos marinos *Arctocephalus australis* y *Otaria flavescens*, Isla de Lobos, Uruguay, en febrero de 1981. Bol. Soc. Zool. Uruguay 2(2):32-35.

XIMENEZ, I.
1962. Frecuencia y fluctuaciones estacionales en la poblacion de *Arctocephalus australis* en algunas zonas de la Isla de Lobos. Rev. Inst. Invest. Pesq. Fac. Vet., Uruguay. 1(2):141-158.

Presence of the South American Fur Seal, *Arctocephalus australis*, in Northern Chile

CARLOS GUERRA C.
Instituto de Investigaciones Oceanologicas
Universidad de Antofagasta
Camino a Coloso S/N, Casilla 1240
Antofagasta, Chile

DANIEL TORRES N.
Instituto Antártico Chileno
Luis Thayer Ojeda 814, Correo 9
Santiago, Chile

ABSTRACT

After an individual of *Arctocephalus australis* was discovered on the coast of Antofagasta (lat. 23°35′S) in 1982, a census during February 1983 revealed 228 animals between Punta Paquica (lat. 21°54′S) and Rocas Abtao (lat. 23°05′S), with 61% of individuals at these two localities. It is suggested that the presence of *A. australis* in northern Chile may be due to an influx from colonies in southern Peru, perhaps caused by the adverse effects of the "El Niño" phenomenon. The distribution and abundance of *A. australis* in Chile is poorly known, and further surveys and research studies are badly needed. In view of the extensive overlap in range and potential confusion between this species and the South American sea lion *Otaria flavescens*, which can legally be shot, it is recommended that the statutory protection be enhanced by a program of education on a local and regional basis to ensure the effective protection of *A. australis*, especially if breeding colonies become established.

INTRODUCTION

Four species of fur seals have been recorded in Chile: Antarctic fur seal *Arctocephalus gazella*, Subantarctic fur seal *A. tropicalis*, Juan Fernandez fur seal *A. philippii*, and South American fur seal *A. australis*.

A. gazella has been recorded at the Juan Fernandez Archipelago (Torres 1983) and might occur regularly during fall and winter in the southern channels (Torres 1976) as suggested by the discovery of a dead individual at Hoste Island (lat. 55°30′S, long. 68°97′W) originally marked at Bird Island, South Georgia (Texera 1974).

A. tropicalis has occurred at the Juan Fernandez Archipelago from 1979 (Torres and Aguayo 1984) to 1984 (Torres 1984, 1987), where a breeding colony could possibly develop, as suggested by the presence of animals of both sexes, including juveniles. It might also occur at other localities between the Diego Ramirez Islands and the Juan Fernandez Archipelago.

A. philippii is endemic to the Juan Fernandez Archipelago and Islas Desventuradas (San Felix and San Ambrosio); no sightings were recorded outside these islands until at least two individuals were identified in colonies of *A. australis* in Peru (P. Majluf, Univ. Cambridge, pers. commun. 1984). It is also possibly found in central and northern coast of Chile.

A. australis was known to breed from the Diego Ramirez Islands north to Chiloe Island (Torres et al. 1979). Although Repenning et al. (1971) and Vaz-Ferreira (1976, 1979) indicate a continuous distribution along the Chilean coast, there is no real historical evidence for its presence in central and northern Chile.

During observation and census work on South American sea lions *Otaria flavescens* (Fig. 1) along the coast of Antofagasta, Chile, a male *A. australis* was photographed (Torres et al. 1983) on islets next to Punta Angamos (lat. 23°05′S) in February 1982. This paper reports the recent findings of this otariid in the area, discusses the possible causes of its presence in northern Chile, and suggests action to ensure its protection.

MATERIALS AND METHODS

The observations made between Punta Paquica and Punta Angamos in February 1983 involved a census of both *A. australis* and *O. flavescens*. Counts were made with the naked eye or using 10×50 binoculars either from small fishing boats or from cliffs.

In August 1983, a skull of an adult male was collected at Punta Angamos; to identify the species, measurements of the facial angle (FA) and condylobasal length (CBL) were made, following Repenning et al. (1971).

RESULTS

The identification of the first animal was made on the basis of photographs (Fig. 2; Torres et al. 1983). This was confirmed when measurements of the FA/CBL ratio of another individual agreed with those of *A. australis* (Fig. 3). Furthermore, when comparing the shape of the postcanines of the skull collected with those illustrated by Repenning et al. (1971), the identity with *A. australis* was clear. The weak teeth are narrower than those of other species and show conspicuous small cusps accessory to the central cusp and diagnostic.

In the area covered, *A. australis* was reported in 13 colonies out of 22 (Figs. 4, 5); the remaining nine colonies were exclusively

Figure 1—Male and female of *Otaria flavescens* at a typical site on the shore of Antofagasta. (Photo: C. Guerra).

Figure 2—Young male of *Arctocephalus australis* on rookery of the shore of Antofagasta. Note the steep substrate (Photo: C. Guerra).

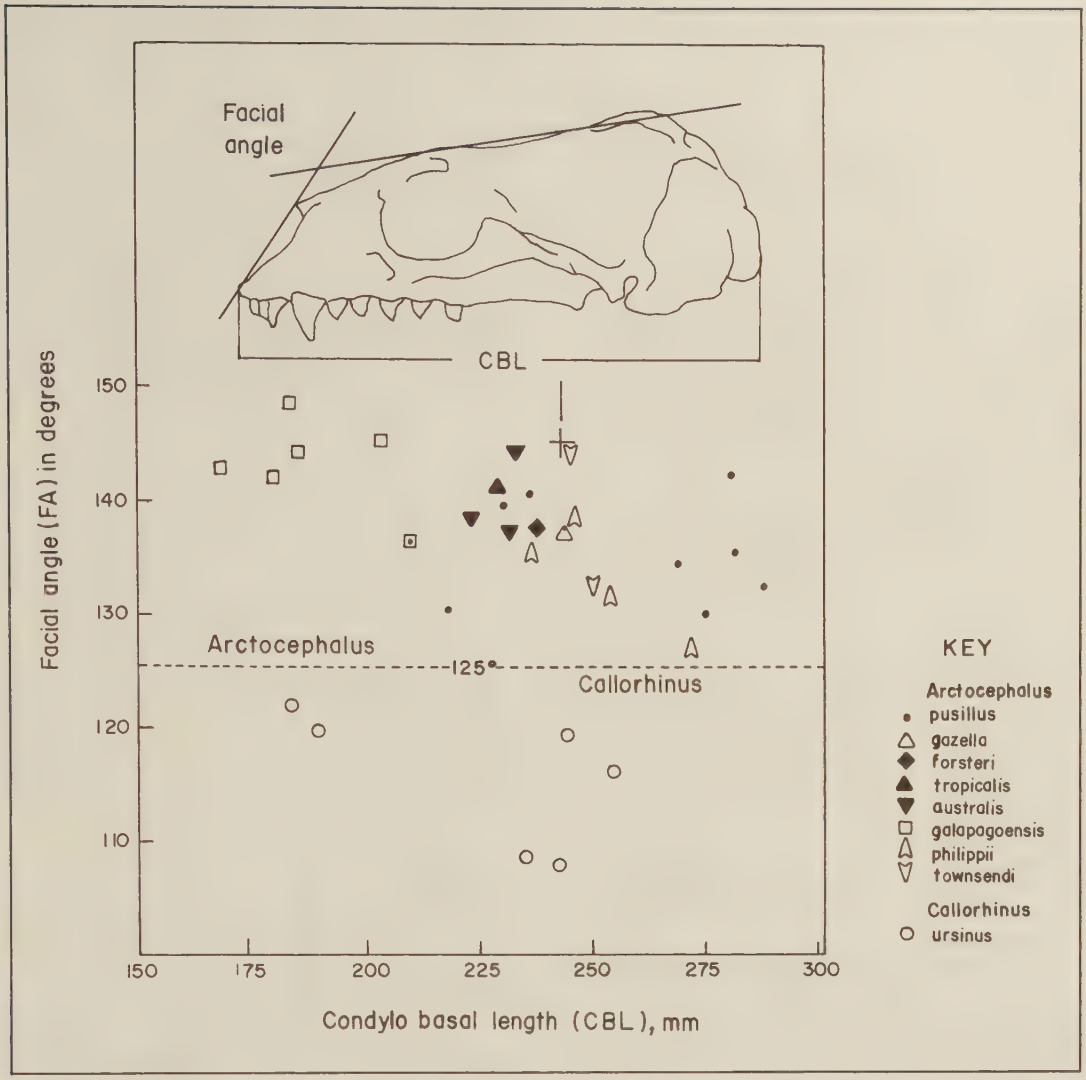


Figure 3—Graph of facial angle (FA) vs. condylobasal length (CBL) of *A. australis* and the other species *Arctocephalus*, after Repenning et al. (1971). The arrow shows the FA/CBL relationship for the skull collected at Punta Angamos, Antofagasta.

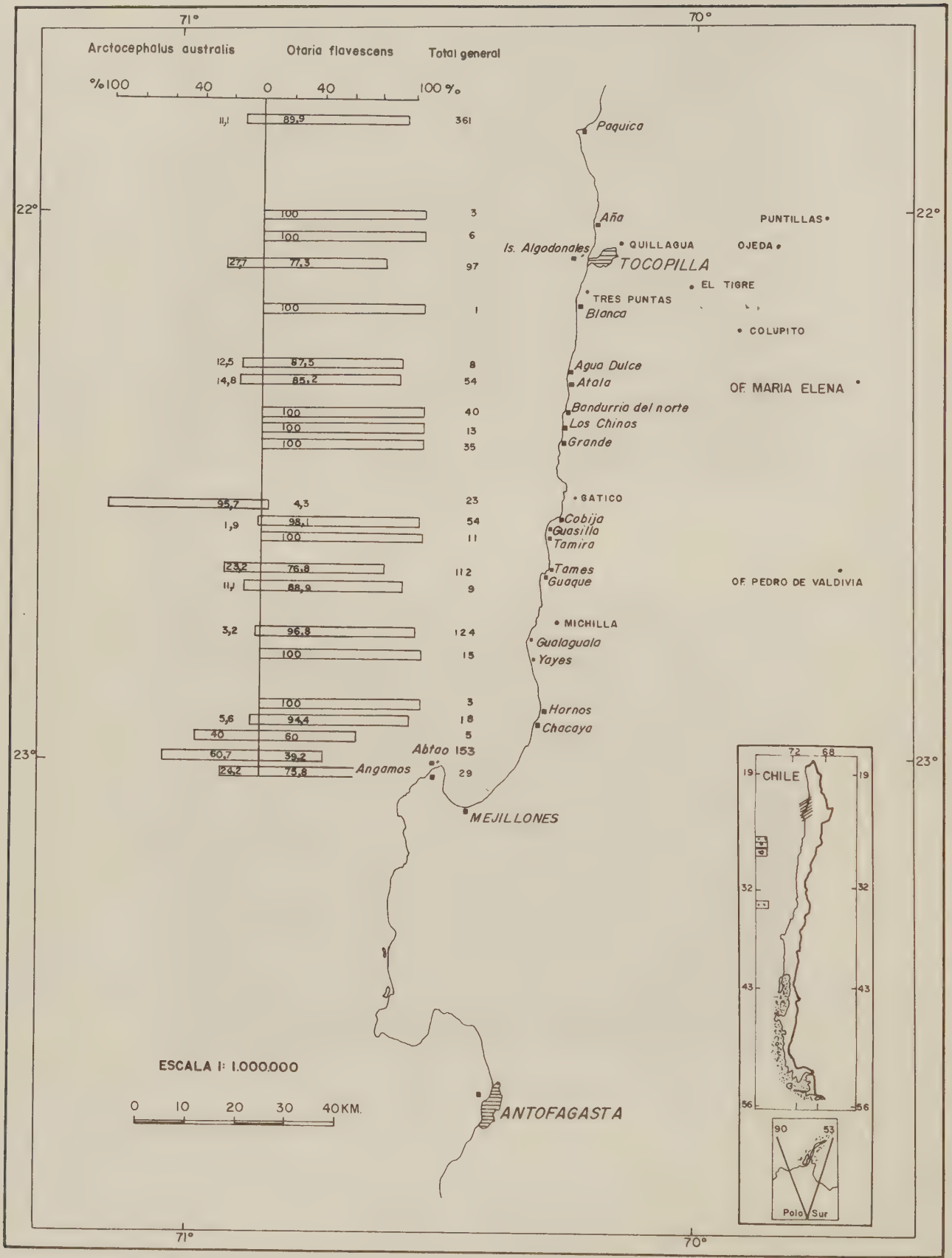


Figure 4—Comparison of distribution and numbers of *A. australis* and *O. flavescens* in northern Chile.

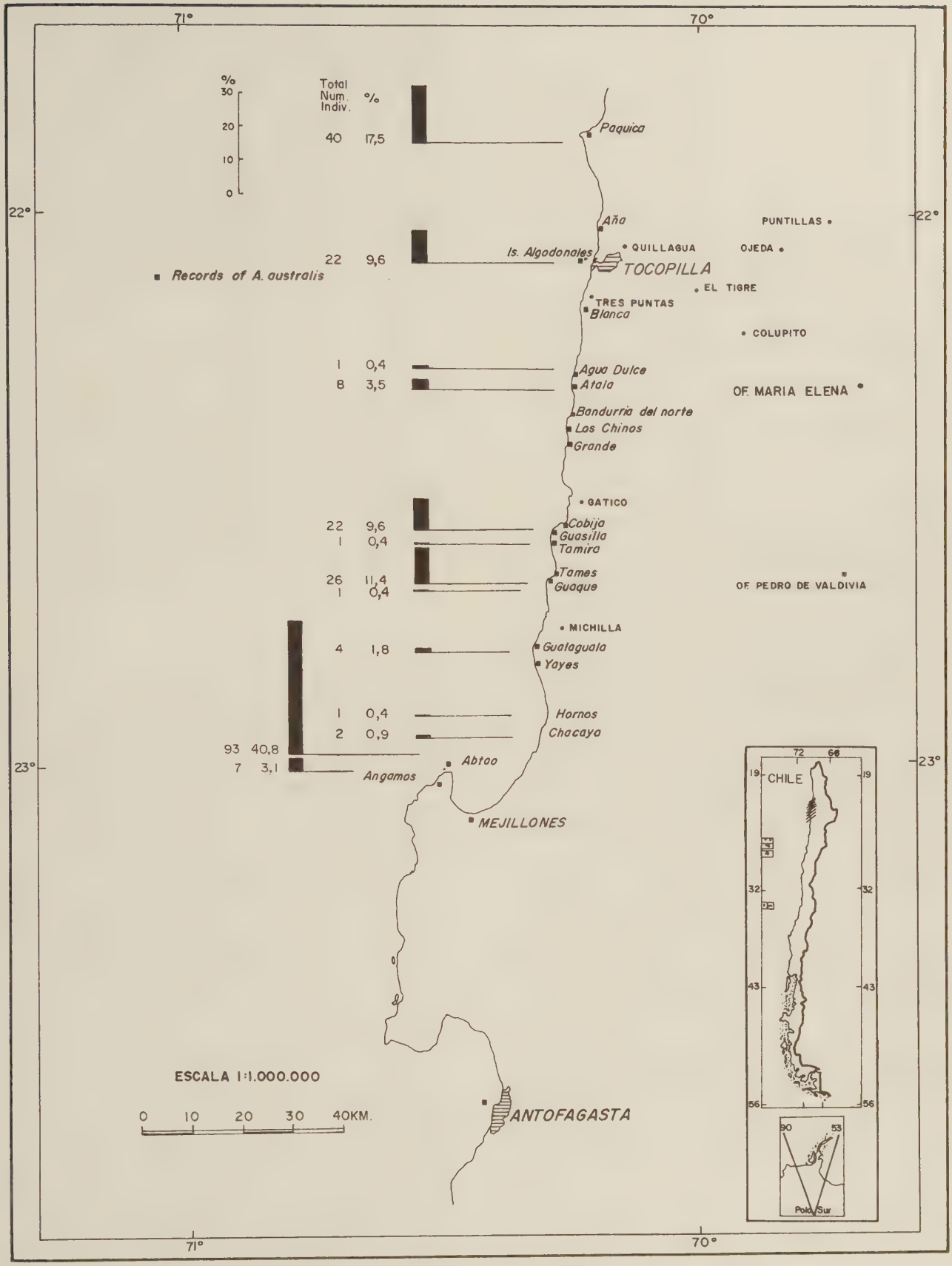


Figure 5—Numerical and percentage distribution of *A. australis* in northern Chile.

Table 1—Distribution and number of the fur seal (*Arctocephalus australis* on the Chilean coast from 21°54′S to 23°05′S during El Niño 1982-83.

Location (°S)	Lat. (°S)	Date	Total no.	%
[a]Pta. Paquica	21°54′	14/02/83	40	17.5
[b]I. Algodonales	22°05′	13/02/83	22	9.6
[a]Pta. Agua Dulce	22°15′	15/02/83	1	0.4
[a]Pta. Alala	22°17′	15/02/83	8	3.5
[a]Pta. Cobija	22°33″	10/02/03	22	9.6
[b]Pta Guasilla	22°35′	10/02/83	1	0.4
[a]Pta. Thames	22°39′	16/02/83	26	11.4
[a]Pta. Guaque	22°41′	16/02/83	1	0.4
[a]Pta. Guala-guala	22°46′	16/02/83	4	1.8
[b]Rocas Blancas	22°56′	17/02/83	1	0.4
[a]Pta. Chacaya	22°58′	17/02/83	2	0.9
[a]Pta. Angamos	23°05′	27/02/83	7	3.1
[b]Rocas Abtao	23°05′	27/02/83	93	40.8
		Total	228	99.8

[a]Individuals on rocks on the shore.
[b]Individuals on islets.

of *O. flavescens*. Figure 4 shows the percentage relationship between the species. Of these 13 colonies, 4 are on islets at distances offshore ranging from 100 to 800 m. All sites occupied by *A. australis* are of rocky substrate. In most cases, the animals were found on steep wave-beaten sectors.

Sites with greater concentrations were, in decreasing order: the sector of Punta Angamos (including the islet of Rocas Abtao), 100 animals; Punta Paquica, 40; and Punta Thames, 26. The coordinates of each site and the number and percentage of animals are shown in Table 1. The data on the census and distribution of both species are shown in Table 2.

Although both species shared most of the sites—without ever occurring on the same rock—*A. australis* was found in several sites not occupied by *O. flavescens*. Only at Punta Paquica were the species particularly close together, probably due to the density of individuals there.

DISCUSSIONS

The photographs and skull measurements confirm that the animals found in this region of Chile are *A. australis*. It is useful to review the information on their occurrence in this area.

From Molina's (1782) time until very recently, the presence of *A. australis* between Arica (lat. 18°27′S) and Valdivia (lat. 39°27′S) had never been confirmed. Aguayo et al. (1971) reported: "...to date in Chile we have observed [*A. australis*] only in two locations down in the south...Moreover, we are in a position to assure that this animal does not exist between Arica and Valparaiso, since during the census of seals we have carried out (1965-68) we have not observed a single individual of this species." Later on, Aguayo and Maturana (1973) do not mention this species in the census made between Arica and Punta Maiquillahue (Valdivia). Some authors, however, have accepted, but not confirmed, the presence of this fur seal between Arica and Valparaiso (Cabrera and Yepes 1940; Yanez 1948; Miller and Rottmann 1976) and other specialists indicate this species as continuously present from the far south to the northern region of Chile (Repenning et al. 1971; Vaz-Ferreira 1976, 1979).

Table 2—Comparison of number and distribution of fur seal *Arctocephalus australis* and sea lion *Otaria flavescens* on the Chilean coast between 21°54′S and 23°05′S during El Niño 1982-83.

			A. australis		*O. flavescens*		Total
Location	Lat. (°S)	Date	no.	%	no.	%	no.
Paquica	21°54′	14/02/83	40	11.1	321	88.9	361
Pta. Ana	22°01′	14/02/83			3	100	3
Sur Pta. Ana		14/02/83			6	100	6
I. Algodonales	22°05′	13/02/83	22	22.7	75	77.3	93
Pta. Blanca	22°11′	15/02/83			1	100	1
Pta. Agua Dulce	22°15′	15/02/83	1	12.5	7	87.5	8
Pta. Alala	22°17′	15/02/83	8	14.8	46	85.2	54
Pta. Bandurrias N.	22°25′	16/02/83			40	100	40
Pta. Los Chinos	22°26′	16/02/83			13	100	13
Pta. Grande	22°28′	16/02/83			35	100	35
Pta. Cobija	22°33′	10/02/83	22	95.7	1	4.3	23
Pta. Guasilla	22°35′	10/02/83	1	1.8	53	98.1	54
Pta. Tamira	22°36′	10/02/83			11	100	11
Pta. Thames	22°39′	16/02/83	26	23.2	83	76.8	112
Pta. Guaque	22°41′	16/02/83	1	11.1	8	88.9	9
Pta. Guala-guala	22°46′	16/02/83	4	3.2	120	96.8	124
Pta. Yayes	22°48′	16/02/83			15	100	15
Pta. Hornos	22°55′	17/02/83			3	100	3
Rocas Blancas	22°56′	17/02/83	1	5.6	17	94.4	18
Pta. Chacaya	22°58′	17/02/83	2	40.0	3	60.0	5
Pta. Angamos	23°05′	27/02/83	7	24.2	22	75.8	29
Rocas Abtao	23°05′	27/02/83	93	60.7	60	39.2	153
		Total	228	(19.4%)	946	(80.6%)	1,174

The possible presence of the South American fur seal in the north has been reported in only two locations: (1) Cerro Moreno, near to Antofagasta (Albert 1901); and (2) Azocar rookery, to the south of Antofagasta (Opazo 1926). In both cases no further data are provided to allow verification of these records. Thus, the record of Torres et al. (1983) and the subsequent observations and records constitute the first definite records of *A. australis* in this area. However, the species is locally common in parts of Peru, so it is strange that it should be absent or rare in Chile north of Chiloe.

There are a number of possible explanations. First, the species may have been overlooked in the past and mistaken, by inexperienced observers, for *Otaria*. This does not seem very likely because several experienced biologists have conducted field work in this area. Second, the species might have been eliminated from the area by hunting and have been unable to recolonize. There are no records of fur seals being hunted in this region, however, and one might have expected some recolonization from Peru in the lengthy period since any general exploitation of fur seal species ceased.

This suggests that the appearance of the species in the area may be fairly recent. As fur seals still appear to be absent between Chiloe and Antofagasta, it is likely that the colonists have come from Peru. The main colonies in Peru seem to be closely associated with upwelling areas (Majluf and Trillmich 1981) and, at least in response to the 1983 El Niño, their numbers undergo substantial fluctuations. It is possible that the major environmental changes caused by the El Niño, whereby numbers of fur seals were much reduced at the Peruvian colonies, prompted the dispersal of animals away from these sites and into northern Chile. This does not account for the presence of the single animal in 1982, before El Niño had started, but, as in other *Arctocephalus* species, there is doubtless substantial dispersal of individuals away from breeding colonies at certain times of the year.

Fur seals may have visited northern Chile during previous El Niño events, but if so, apparently did not colonize the area. This might be because the local upwelling is insufficiently strong to support the more pelagic *A. australis*, although the marine environment and its resources are sufficient to support *O. flavescens*. Further surveys are required to determine whether the animals recorded in 1983 stay in the area and attempt to form a breeding colony.

Although all fur seals in Chile are fully protected, *O. flavescens* is not because hunting of animals that interfere with fishery activities is permitted. Local fishermen may not readily be able to distinguish *A. australis* from *O. flavescens*, and a program of local and regional education is required to ensure that *A. australis* remains fully protected in northern Chile and that its attempts to colonize the area are not thwarted.

ACKNOWLEDGMENTS

We thank P. Majluf for her valuable comments on this paper and for translating it into English; Scarlett Marin, George Portflitt, and Rolando Rocco of the Universidad de Antofagasta for their enthusiastic help during the surveys, and Victor Sotomayor, Danilo Araya, Tomas Oviedo, and Carlos Flores for making the marine censuses possible at Mejillones, Cobija, Tocopilla, and Paquica, respectively. The paper was typed by Monica Rojas, to whom the authors are most grateful.

CITATIONS

AGUAYO, A., and R. MATURANA.
1973. Presencia del lobo marino comun (*Otaria flavescens*) en el litoral chileno. I. Arica (18°27′S.) a punta Maiquillahue (39°27′S.). Biol. Pesq. 6:45-75.

AGUAYO, A., R. MATURANA, and R. D. TORRES.
1971. El lobo fino de Juan Fernandez. Rev. Biol. Mar. 14(3):135-149.

ALBERT, F.
1901. Los Pinipedos de Chile. Imprenta, litografia y encuadernacion Barcelona, Santiago de Chile, 59 p.

CABRERA, A., and J. YEPES.
1940. Mamiferos Sudamericanos. Compania Argentina de Editores, Buenos Aires, Argentina, 370 p.

MAJLUF, P., and F. TRILLMICH.
1981. Distribution and abundance of sea lions (*Otaria byronia*) and fur seals (*Arctocephalus australis*) in Peru. Z. Saugetierkd. 46:384-393.

MILLER, S., and J. ROTTMANN.
1976. Guia para el reconocimiento de mamiferos chilenos. Manual expedicion a Chile. Editorial Nacional Gabriela Mistral, Santiago, Chile, 200 p.

MOLINA, G. I.
1782. Saggio sulla storia naturale del Chile. Bologna, 387 p.

OPAZO, A.
1926. Memoria del servicio de pesca maritima y fluvial correspondiente at 1926. Seccion lobos, p. 48-52.

REPENNING, C. A., R. S. PETERSON, and C. L. HUBBS.
1971. Contribution to the systematics of the southern fur seals with particular reference to the Juan Fernandez and Guadalupe species. Antarctic Pinnipedia. Antarct. Res. Ser. 18:1-34.

TEXERA, W. A.
1974. Nuevos antecedentes sobre mamiferos de Magallanes. II. Hallazgo de *Arctocephalus gazella* (Mammalia: Otariidae) en isla Hoste, de la region de Magallanes, anillado en isla Bird, Georgia del Sur. Ans. Inst. Pat. Punta Arenas (Chile) 5(1-2):189-198.

TORRES, D.
1976. Comentarios sobre el informe preparado por el Grupo III Ad-Hoc, relativo a pinipedos y nutrias marinas. *In* Comments on the draft reports of ad-hoc groups I, II, III and IV (ACMRR/MM/SC/2, 3, 4, 5), p. 8-14. ACMRR/MM/SC/Cont. 2, FAO, Sci. Cons. Mar. Mamm., Bergen, Norway.
1983. Reuniones sobre pinipedos realizadas en Pretoria por el grupo de expertos de SCAR. Bol. Antart. Chil. 3(2):41-43.
1984. Antecedentes sobre el lobo fino de Juan Fernandez, *Arctocephalus philipii* (Peters, 1866) y proyecciones para su estudio. (Pinnipedia: Otariidae). Intl. Symp. and Workshop on the Biology of Fur Seals, Cambridge, U.K., April 1984.
1987. Juan Fernandez fur seal, *Arctocephalus philippii*. *In* Croxall, J. P., and R. L. Gentry (eds.), Status, biology, and ecology of fur seals, p. 37-41. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 51.

TORRES, D., and A. AGUAYO.
1984. Presence of *Arctocephalus tropicalis* (Gray, 1872) at the Juan Fernandez Archipelago, Chile. Proc., Third Intl. Theriological Congr., Helsinki, 15-20 August 1982. Acta Zool. Fenn. 172:133-134.

TORRES, D., C. GUERRA, and M. SALLABERRY.
1983. El lobo fino del sur, *Arctocephalus australis*, en el norte de Chile. Bol. Antart. Chil. 3(1):23-24.

TORRES, D., J. YANEZ, and P. CATTAN.
1979. Mamiferos marinos de Chile: Antecedentes y situacion actual. Biol. Pesq. 11:49-81.

VAZ-FERREIRA, R.
1976. *Arctocephalus australis* (Zimmermann). South American fur seal. ACMRR/MM/49. FAO, Sci. Cons. Mar. Mamm., Bergen, Norway, 13 p.
1979. South American fur seal. *In* Mammals in the seas, p. 34-36. FAO Fish. Ser. 5, vol. 2.

YANEZ, P.
1948. Vertebrados marinos chilenos. I. Mamiferos. Rev. Biol. Mar. 1(2):103-123.

Fur Seals, *Arctocephalus* spp., at Macquarie Island

PETER D. SHAUGHNESSY
CSIRO
Institute of Biological Resources
Box 225
Dickson ACT 2602
Australia

L. FLETCHER
Antarctic Division
Channel Highway
Kingston, Tasmania 7150
Australia

ABSTRACT

Macquarie Island and its fur seals were discovered in July 1810 when indiscriminate harvesting began. Little harvesting occurred after 1820. As many as 193,300 fur seals were killed. No specimens are available of the original fur seal (the "upland seal"). Two groups of fur seals at Macquarie Island are now recognized: one comprises New Zealand fur seals *Arctocephalus forsteri*; the other includes subantarctic *A. tropicalis* and Antarctic fur seals, *A. gazella*. Of these species, it is deduced that *A. tropicalis* is most likely to have been the upland seal. *A. forsteri* has been at the island since at least 1948. It is present year-round, does not breed there, and is the more abundant group. Numbers increase slowly from November to March. Annual censuses in about March increased since 1950, reaching 1,222 for the whole island in 1982. From 1981-82 breeding territories containing cows and pups of *A. gazella* and *A. tropicalis*, as well as *A. tropicalis* bulls, have been recognized. *A. tropicalis* has not previously been reported as breeding in Australian waters. It is likely that pups born since 1954-55 belong to the *A. gazella*/*A. tropicalis* group and not to *A. forsteri* as previously assumed. Maximum numbers in the *A. gazella*/*A. tropicalis* group occur in summer. In 1982-83, 20 pups were born. Data are provided on pupping season; mortality, nursing period, mass, and growth of pups; and the attendance patterns of cows ashore. For seals of both groups information is provided on spatial and temporal distribution and feeding habits. Suggestions are made for further work to assist in identifying pups of the three species, to determine which species partake in mating, and to monitor an expected population increase.

INTRODUCTION

Fur seals were abundant at Macquarie Island (lat. 54°S, long. 159°E, close to and north of the Antarctic Convergence; Fig. 1) when it was discovered in 1810. Intense, indiscriminate harvesting began immediately, and the fur seals were reported extinct by 1820. Few were taken in ensuing years (Cumpston 1968). There are no known specimens of the original seal, nor is its specific identity known.

By 1948 when the Australian National Antarctic Research Expedition (ANARE) station was installed on the Isthmus, the New Zealand fur seal, *Arctocephalus forsteri*, was established at the island (Gwynn 1953). This species breeds on the South Island of New Zealand, its subantarctic islands, and on the coast of South Australia and Western Australia (Crawley and Warneke 1979).

The first fur seal pup was found at Macquarie Island in March 1955 (Csordas 1958). Small numbers (up to two, possibly three, annually) were born from then until 1963-64 (Csordas and Ingham 1965). These pups were assumed to be *A. forsteri*. A male Subantarctic fur seal, *A. tropicalis*, was reported at Macquarie Island on North Head Peninsula in March 1959 by Csordas (1962) who used the vernacular name, Kerguelen fur seal.

In this paper the history of fur seal harvesting at the island is reviewed, and counts of all fur seals found there are brought up

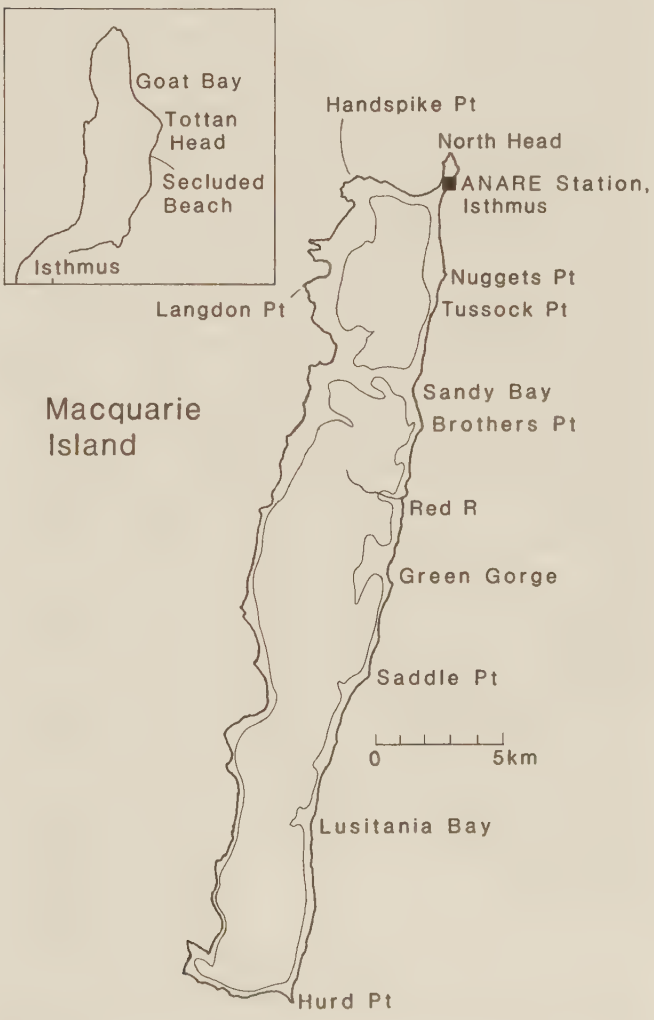


Figure 1—Map of Macquarie Island showing localities where fur seals occur.

to date. Furthermore, the presence of breeding groups comprising the Antarctic fur seal *A. gazella* and *A. tropicalis* since the summer of 1981-82 is documented, and aspects of the biology of all fur seals at the island are presented.

Shaughnessy was stationed at the island in 1966 and 1968, visited it in December 1981, and subsequently collated information from fur seal log books kept by ANARE personnel. Fletcher was the resident medical officer from October 1981 to February 1983, and made most of the observations from that period included in this report.

HISTORY OF HARVESTING

No detailed enumeration of fur seal skins taken at Macquarie Island has been made, and information summarized here is almost entirely from Cumpston (1968). Fur seals and southern elephant seals, *Mirounga leonina*, were abundant at the island when it was discovered. There appears to be little confusion in the literature between harvest statistics of the two species because the former was taken for skins, whereas the latter was taken for oil and, less importantly, for hides. It seems that the terms "seals" and "skins" have been used for fur seals, and the terms "sea elephants", "oil," and "hides" for elephant seals.

Harvesting began at Macquarie Island when it was discovered in July 1810 by the sealing vessel *Perseverance* from the Sydney merchant house of Robert Campbell and Co. By 25 May 1811, 56,974 skins had been procured, with another 5,000 taken between May and October 1811. Two secondhand reports suggest that 80,000 to 100,000 seals were taken in the first year, possibly involving ships of other Sydney merchants (e.g., Simeon Lord).

Cumpston (1968, p. 26) concluded that "By the end of 1812 over 120,000 seal skins had been exported," but elsewhere (Cumpston 1974, p. 34) noted that "In 2 years 160,000 fur seal skins had been shipped." These figures presumably refer to the first 18 months and 2 years of harvesting; it is not apparent how they were obtained. After 1812, catches were much smaller. For the summer of 1813-14, Cumpston (1968) records only a single shipment of 345 skins. For the following summer he again records only one shipment of 2,690 skins (Cumpston 1968), although the *Sydney Gazette* of 15 April 1815 indicated that more (up to 5,000 or 6,000) were taken.

By 1815 fur sealing at Macquarie Island was no longer a paying proposition, according to the *Sydney Gazette* of 15 April 1815 (Cumpston 1968). Even so, 10,516 skins were sent to Sydney in March 1819 on the *Governor Bligh*, some of which were from Macquarie Island, and 4,433 skins from Macquarie arrived there in May and November 1819 on the *Elizabeth and Mary*. But in the following year the skipper of the *Campbell Macquarie* found no fur seals there (Cumpston 1968).

After his visit to the island in late 1820 the Russian explorer Bellingshausen stated that fur seals had been exterminated (Debenham 1945). This seems surprising in view of three substantial shipments of skins that arrived in Sydney during the previous year and the report of 12,000 arriving in Sydney in February 1821 on the *Governor Bligh* (Cumpston 1968). It is possible that some of those skins had been collected earlier and retained at the island for want of shipping. In 1821 four fur seals were reported to have been killed by Captain Raine of the sealer *Surry*. A few years later, two sealing expeditions to Macquarie Island, one in 1829 (*Governor Arthur*) the other in 1831 (*Venus*), failed to find any fur seals (McNab 1909, 1913). Similarly none was seen from December 1851 to April 1852 by a party led by John Cook collecting elephant seal oil (Cumpston 1968). On the other hand, an Enderby exploring expedition is reported to have taken a very large number of fur seal skins there in 1837, but no details are given (Cumpston 1968).

Summation of the harvest data provided by Cumpston (1968 and 1974) leads to an overall harvest of at least 179,500 to 193,300 skins. These estimates are similar to the figure of 180,000 skins quoted by Carrick (1957) and Csordas and Ingham (1965). The source of that figure is not stated but is likely to have been Mawson (1923). The firm of Robert Campbell and Co. alone took at least 101,200 skins (Hainsworth 1972). Higher estimates rest on an interpretation of the early secondhand account in the *Sydney Gazette* of 15 April 1815 (Cumpston 1968, p. 35) that "100,000 skins were procured in the season" for each of several years from the island's discovery. This interpretation is discounted, since it is clear from the whole article that a harvest figure is provided for the first season only.

Until 1919, Macquarie Island was inhabited periodically by gangs of men collecting oil from elephant seals and penguins. It was then visited rarely until 1948 when the Australian government set up the permanent ANARE station. Few fur seals were reported until 1948. Recorded sightings were made in 1874, and between 1896 and 1900 (Cumpston 1968). Members of the Australasian Antarctic Expedition (AAE) residing at the island from December 1911 to November 1913 saw none (Mawson 1915), but were informed that over the previous 11 years a few fur seals (all of which were killed) had appeared on the beaches on a number of occasions (Mawson 1943). The last license for harvesting elephant seals and penguins at Macquarie Island was issued for 12 months beginning August 1918. The island was declared a sanctuary in 1933 (Cumpston 1968).

In summary, harvesting of fur seals at Macquarie Island began in 1810; by 1815 it was hardly a paying proposition; and little was done after 1820. The precise number killed is not known, but is likely to have been as many as 193,300. Few fur seals were seen at the island from 1820 to 1948, and most of those were killed by gangs taking elephant seals and penguins for oil, which ensured extinction of the original fur seal and prevented any colonizers from becoming established. Early accounts (Cumpston 1968) indicate that killing was indiscriminate. The specific identity of the fur seal so energetically harvested at Macquarie Island is unknown.

SUBSEQUENT AND PRESENT RECORDS

As indicated above, a population of *A. forsteri* has been at Macquarie Island since at least 1948, and one *A. tropicalis* was reported there in 1959. In December 1981 two *A. tropicalis* adult males were discovered holding breeding territories. This led to a closer study of all fur seals on the island, a reassessment of their taxonomic status, and an examination of fur seal log books. Two distinct groups of fur seals are now considered to dwell at Macquarie Island, one comprising *A. forsteri*, the other including both *A. gazella* and *A. tropicalis*. The two last species breed on islands in the South Atlantic and South Indian Oceans: the former south of and near the Antarctic Convergence, the latter north of the Antarctic Convergence. Major concentrations are found at South Georgia and Gough Island, respectively. The two species occur together at Marion Island and Iles Crozet (Bonner 1968; Condy 1978; Jouventin et al. 1982; Shaughnessy 1982).

Arctocephalus forsteri is generally the most abundant species at Macquarie Island. It is present year-round, but does not breed there.

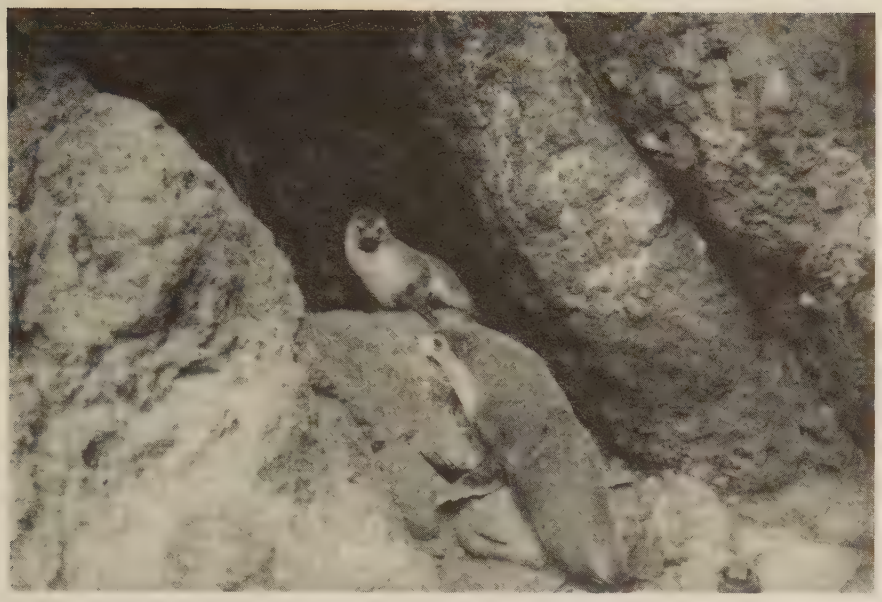


Figure 2—Subantarctic fur seal bull and cow, and Antarctic fur seal pup in Goat Bay, Macquarie Island, January 1983.

Most animals were reported to be young, nonbreeding males (Johnstone 1972). They occur primarily at North Head Peninsula, on the east coast of the island and on the northwest and southeast points.

Current composition of breeding territories

Breeding territories were observed in 1981-82 and 1982-83 at Goat Bay and Secluded Beach on the east coast of North Head Peninsula (Fig. 1). The two *A. tropicalis* bulls discovered in December 1981 were identified by the unique cream-colored chest and face and black crest of that species' adult male (see Bonner 1968; Repenning et al. 1971; Condy 1978). The remainder of their pelage was dark grey to dark brown and recognizably different from that of New Zealand fur seals on North Head Peninsula, which have a more uniform, browner pelage like those in the New Zealand region (Crawley and Wilson 1976). *Arctocephalus tropicalis* bulls were seen again in 1982-83 (Fig. 2). No bulls seen in these two seasons fitted the descriptions of *A. gazella* provided by Bonner (1968) and Condy (1978).

In December 1981 Shaughnessy photographed seven cows in one of the territories. Those not obscured were later identified from transparencies by W. N. Bonner (Br. Antarct. Surv., Cambridge), D. W. Doidge (McGill Univ., Quebec, Can.), and G. I. H. Kerley (Mamm. Res. Inst., Univ. Pretoria) (pers. commun. 12 May and 28 June 1983) as *A. gazella* because of their long flippers, prominent light-colored ears, and almond-shaped eyes, characteristics mentioned by Condy (1978). An *A. tropicalis* cow was identified in a black-and-white print taken at Goat Bay in January 1983 (Fig. 2) by its pelage coloration: pale on the face, throat, and chest contrasting with darker head and back (G. I. H. Kerley, Univ. Pretoria, pers. commun. 25 April 1984). The flat head, white muzzle, and blunt snout of the pup in the same print serve to identify it as *A. gazella*. The evidence suggested it did not belong to the *A. tropicalis* cow. In general, cows in territories in 1981-82 and 1982-83 had sleek, silvery-gray dorsal pelage, with a paler ventral surface, and were readily differentiated from *A. forsteri* animals of similar size which have a more uniform, browner pelage (Crawley and Wilson 1976).

Vocalizations of fur seals in breeding groups at Secluded Beach were recorded in January 1976 by D. Parer, Australian Broadcasting Comm., Melbourne. A sonogram of the pup-attraction call of a cow (Fig. 3) is similar to that of *A. gazella*, and different from those of *A. p. doriferus* and *A. forsteri* featured by Stirling and Warneke (1971; Fig. 1). Sonograms of *A. tropicalis* were not available for comparison.

A few of the pups in territories held by an *A. tropicalis* bull and including *A. gazella* cows were photographed. Some of them had relatively long flippers, a broad, flat head, a blunt snout, and whitish muzzle, which made them similar in appearance to *A. gazella* pups at South Georgia, as illustrated by Bonner (1968, plates IIIb and Vf). The whitish muzzle of the *A. gazella* pup has also been noted at Marion Island by Condy (1978) and G. I. H. Kerley (Univ. Pretoria, pers. commun. 15 Aug. 1983) and contrasted with the muzzle of the *A. tropicalis* pup which is the same color as the remainder of the face. The muzzle of some *A. forsteri* pups is also grizzled (R. H. Mattlin, Fish. Res. Div., Wellington, NZ, pers. commun. 25 April 1984). The head of *A. gazella* pups, which is broad and flat and has a blunt snout, appears different in shape from those of two *A. forsteri* pups depicted in photographs taken at South Neptune Island, South Australia by I. Stirling (Can. Wildl. Serv., Edmonton, Alberta) and at Open Bay Islands, New Zealand, by R. H. Mattlin (Fish. Res. Div., Wellington, NZ). Heads of those pups have a rounded profile and sharper nose.

Of the pups photographed at Macquarie Island in 1982-83, the flippers of one were shorter than those of *A. gazella* pups, but it could not be identified to species. In another, the flipper length and white muzzle were suggestive of *A. gazella*, but the face profile was not blunt as in *A. gazella* pups. Thus, although several pups have been identified as *A. gazella*, we consider that not all of them in 1982-83 belonged to that species. Some of them that cannot be identified may be hybrids between *A. gazella* cows and *A. tropicalis* bulls.

No *A. forsteri* bulls or cows were found in territories during the breeding season in 1981-82 and 1982-83. We conclude, as did Johnstone (1972), that the species occurs at the island only as a nonbreeding population.

In summary, seals in breeding territories at Macquarie Island were not *A. forsteri*. All bulls could be identified as *A. tropicalis*. Both *A. gazella* and *A. tropicalis* cows were recognized, as well as *A. gazella* pups. But only a small number of cows and pups could be identified, and we believe that *A. tropicalis* pups were also at the

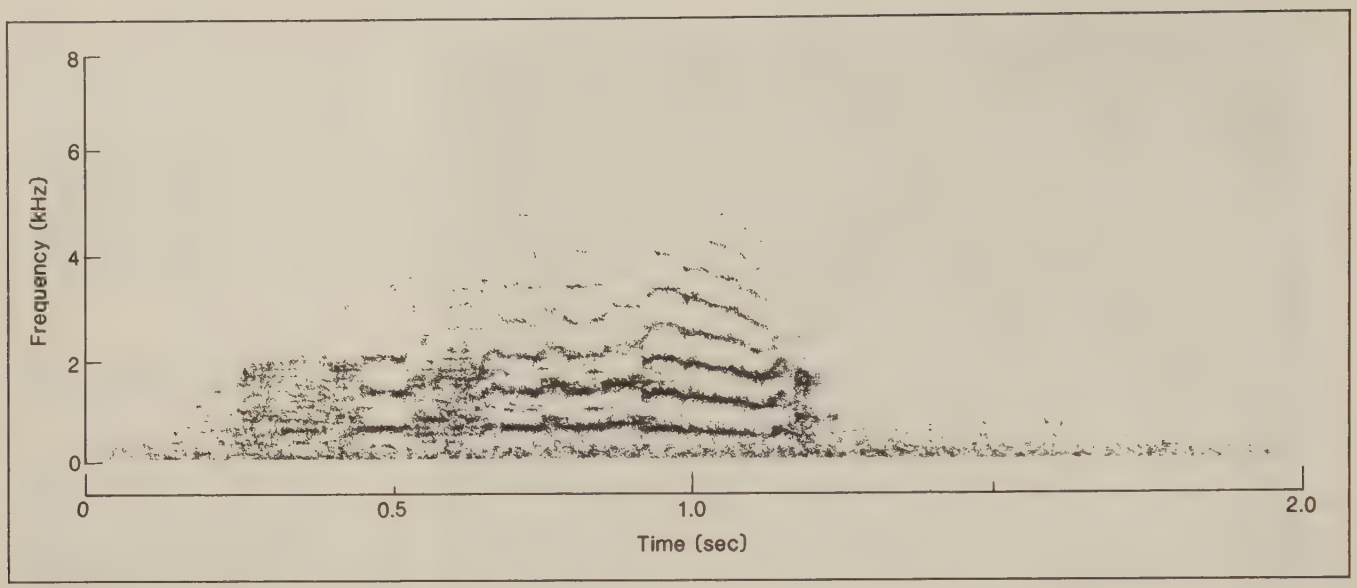


Figure 3—Sonogram of pup-attraction call of a cow at Macquarie Island, January 1976 (cf. *A. gazella* cow in Stirling and Warneke 1971, fig. 1d).

island, based on the length of time they were ashore (see below). For convenience, seals in territories are referred to in this paper as the *A. gazella*/*A. tropicalis* group.

Behavior outside the breeding season

On a few occasions in 1981-82, *A. forsteri* males were seen with cows and pups of the *A. gazella*/*A. tropicalis* group after *A. tropicalis* bulls had abandoned them. No such groups were seen in 1982-83.

The haul-out pattern of seals of the two groups at Macquarie Island during winter was quite different. With the exception of young-of-the-year, animals of the *A. gazella*/*A. tropicalis* group were not seen ashore in 1982 after June, and no bulls or subadult males were ashore after May. On the other hand, *A. forsteri* were ashore year-round, although few were present from July to November. These were mostly subadult males and, to a lesser extent, immatures.

Identity of pups born since 1955

Pups are known to have been born at Macquarie Island since 1954-55. Earlier they were assumed to be *A. forsteri* because older animals at the island had been so identified by E. Troughton of the Australian Museum, Sydney (Gwynn 1953). Although we have looked closely at pups and their attendant cows only in 1981-82 and 1982-83, we suggest that pups born earlier have not been *A. forsteri*. Photographs of pups (some with attendant cows) that we examined are all of *A. gazella*. They are: photographs in Csordas (1963) and Csordas and Ingham (1965, plate 4) which we deduce were of pups born in December of 1955 and 1956, respectively; two black-and-white prints and two transparencies by M. D. Murray (CSIRO, Sydney) of a pup in December 1957; a transparency of a pup by W. J. M. Vestjens (CSIRO, Canberra) in 1962; a transparency by J. K. Ling (S. Aust. Mus., Adelaide) of a pup in February 1964; a transparency by P. J. Ormay (formerly of ANARE, Melbourne) of a cow and pup in December 1967; and a transparency by G. W. Johnstone (Antarct. Div., Hobart) of a cow and pup in December 1975. Each photograph shows a pup with the flat head, whitish muzzle, and blunt snout characteristic of *A. gazella*. In addition, a transparency of a cow with barely visible pup taken in December 1981 shows the long flippers characteristic of *A. gazella*. Each of the photographs taken in December 1955, 1956, 1967, and 1975 includes an *A. gazella* cow.

Earlier sightings of *A. gazella* and *A. tropicalis*

Individual male subantarctic fur seals had been sighted at Macquarie Island before the discovery of breeding groups there in December 1981. One such male was reported by Csordas (1962). Confirmation that this was an *A. tropicalis* is provided by the similarity of its description and photograph with those described above and in Figure 2. We are aware of sightings of seven other *A. tropicalis*, all from North Head Peninsula, in December 1961, February and March 1963, September 1963, March 1965, February 1968, December 1973 and March 1974 (probably of the same animal), and December 1978. The first of these had the coloration of an *A. tropicalis* cow. All others had the creamy white chest and face typical of *A. tropicalis* males. The skull of the second animal was collected (Museum of Victoria no. C3995).

An immature *A. gazella* was sighted on the Isthmus at the ANARE station on several occasions in September 1980. It was identified on the basis of its long flippers and prominent ears. Five sightings of *A. gazella* cows are included in the previous section.

Use of transferrin types in identification

Identifying seals of the *A. gazella*/*A. tropicalis* group is not assisted by information currently available on electrophoretic typings of the blood serum protein transferrin by Shaughnessy (1970), although 30 samples from Macquarie Island were examined. Transferrin has also been examined in *A. gazella* and *A. tropicalis* from Marion Island by Kerley (1984) who demonstrated a marked difference between the two species. No comparison was made with transferrin types reported by Shaughnessy (1970). Thus transferrin types of the three species occurring at Macquarie Island have been demonstrated, although at different islands. An orchestrated survey of series from the island and from reliable sources of the three species involved could be used to resolve the species composition of fur seals at Macquarie Island.

IDENTITY OF THE ORIGINAL SEAL OF MACQUARIE ISLAND

According to the French taxonomist Lesson (1828) the original seal at Macquarie Island was known to Anglo-American sealers as the "Upland seal." It also occurred at the Antipodes Islands (lat. 50°S, long. 175°E). Its name implies that it moved well inland, a habit characteristic of *A. gazella* at South Georgia (D. W. Doidge, McGill Univ., Quebec, and T. S. McCann, Br. Antarct. Surv., Cambridge, pers. commun.) and Marion Island (G. I. H. Kerley, Univ. Pretoria, pers. commun.); *A. tropicalis* at Marion Island (Kerley, pers. commun.); A. forsteri in New Zealand and on its subantarctic islands (Crawley and Wilson 1976).

At least some of the upland seal population must have been ashore during winter, for fur seals were present in July 1810, when Macquarie Island was discovered, and were ashore again in the following winter when 5,000 skins were taken between May and October. According to Condy (1978) and Kerley (1983a) the small population of *A. gazella* at Marion Island is rarely ashore during winter. Males of this species come ashore in winter at Bird Island, South Georgia, although in much smaller numbers than during the breeding season (Payne 1979; P. G. Copestake, Br. Antarct. Surv., Cambridge, pers. commun.). This aspect of the upland seal's annual cycle suggests that it was not *A. gazella*.

That the original fur seal at Macquarie Island is unlikely to have been *A. forsteri* is suggested by the failure of the colonizing *A. forsteri* population, which has been there since at least 1948, to establish a breeding population and increase markedly, even though the habitat appears unchanged. Lesson (1828, p. 411) described the upland seal as small and distinguished it from the fur seal harvested in southern New Zealand which "appears to have distinct characters." On the basis of location, the latter seal was most likely *A. forsteri*. Consequently, according to Lesson, the original species at Macquarie Island was not *A. forsteri*. When writing of the upland seal, Falla (1965, p. 67) stated that it was reputed to have had a "superior fur." In addition he noted that a collection of seal bones was "made some time ago by the Australian Expedition at Macquarie I., but not yet studied."

A collection of bones was not mentioned by Mawson (1940, 1942, 1943) in reviews of the work of the Australasian Antarctic Expedition (AAE) at Macquarie Island; by Ainsworth (Mawson 1915) who was leader of the party at Macquarie; by Grenfell Price (1962) in his account of the British, Australian, and New Zealand Antarctic Research Expedition (BANZARE); or by Falla in his report of animal life seen at the island during the BANZARE visit (Crowther 1933). Further evidence that the collection is unlikely to have been made on either of these expeditions comes from an examination of records held in the Mawson Institute for Antarctic Research, Adelaide, Aust., and enquiries made of appropriate museums.

Falla visited the island in December 1957, and it is likely that he was referring to a collection made there in that year, even though it was only a few years later in 1965 that he mentioned that the bones were collected "some time ago." M. P. Hines (formerly of ANARE, Melbourne, pers. commun. 6 June 1984) collected two fur seals of unknown identity in 1957 which are deposited in the National Museum of New Zealand (two skeletons, one skin; nos. MM 1640 and MM 1641). In addition, K. Keith (formerly of ANARE, Melbourne, pers. commun. 30 May 1984) collected one fur seal. These specimens are all of animals that died during 1957 and so provide no information on the identity of the upland seal.

Fur seals were greatly reduced by harvesting in the nineteenth century in New Zealand, its subantarctic islands, and Macquarie Island (Crawley and Warneke 1979). They became extinct only at Antipodes and Macquarie Islands (Taylor 1969; Falla 1962, 1965), the two islands where the upland seal occurred. *A. forsteri* did not become extinct at any of the New Zealand subantarctic islands. Presumably the rugged coastline it inhabited made harvesting the last few animals uneconomical (Falla 1962) when there were no alternative species to continue harvesting, as there were at Macquarie Island.

Both Macquarie and Antipodes Islands have been recolonized by fur seals this century. As at Macquarie, the colonizers at the Antipodes are nonbreeding *A. forsteri* (Taylor 1969). The numbers remain small, at 1,100 in February 1969 (Taylor 1979), especially in comparison with the presumed original numbers (Crawley and Warneke 1979). Numbers of fur seals at the Antipodes Islands are now similar to those at Macquarie Island and, furthermore, appear to have increased at a similar rate from very small numbers in 1950. These observations support the proposition that the original fur seal at Macquarie was not *A. forsteri*.

Csordas (1962) suggested that the upland seal may have been *A. tropicalis*, based on his sighting of a "young male" *A. tropicalis* at Macquarie Island in March 1959. He further suggested that it was gradually rediscovering its old colonies. Falla (1965) echoed these sentiments, although he used the name *A. gazella*, as used then for the seal reported by Csordas.

The sighting of a male *A. tropicalis* at the Antipodes Islands in December 1978 by Taylor (1979) provides some support for the proposition that this species is the upland seal, although stragglers of *A. tropicalis* are not limited to Macquarie and Antipodes Islands. However, although the arguments presented here favor the proposition that *A. tropicalis* is more likely to have been the upland seal than *A. gazella* or *A. forsteri*, the possibility remains that it was another, extinct species of fur seal.

STATUS AND BIOLOGY OF *A. FORSTERI* AT MACQUARIE

Spatial distribution

Both Csordas and Ingham (1965) and Johnstone (1972) reported that most fur seals at Macquarie Island were on North Head Peninsula. The same distribution was found in a census carried out over most of the island in early March 1982, at the time of year when maximum numbers of *A. forsteri* are ashore (Table 1). The west coast south of Handspike Point was excluded from the census, since fur seals were not reported there by Csordas and Ingham (1965) and have seldom been seen there in recent years. In the 1982 census a total of 1,222 *A. forsteri* were counted, 70% on North Head Peninsula, where they occupied several rocky coves. This census and others reported here include only animals ashore and exclude those nearby in the sea. No correction has been made for animals ashore but overlooked. *A. forsteri* are more numerous on the east coast of North Head Peninsula, but about one-third of them occur on the west coast during late summer when numbers are maximal. Some of those on the east coast have been observed with the *A. gazella*/*A. tropicalis* group.

Temporal distribution

Numbers of fur seals on North Head Peninsula were highest from mid-February to early April according to Csordas and Ingham (1965) who graphed counts for 5 years between 1949-50 and

Table 1—Counts of fur seals on Macquarie Island, 5-9 March 1982[a].

Location	*A. forsteri*	*A. gazella/ A. tropicalis*
Handspike Point	80	0
North Head Peninsula	845	16
The Isthmus to Sandy Bay[b]	41	0
Sandy Bay to Green Gorge[c]	116	0
1 km south of Green Gorge	32	0
Saddle Point	20	0
Elsewhere between Green Gorge and Lusitania Bay	2	0
Lusitania Bay to Hurd Point	10	0
Hurd Point	76	7
	1,222	23

[a]Excludes the west coast south of Handspike Point.
[b]Most at Tussock Point.
[c]Most at Brothers Point and the mouth of the Red River.

1963-64. Counts made in another 4 years between 1964-65 and 1981-82 (Fig. 4) concurred with those observations. This seasonal distribution is similar to that at nonbreeding colonies (hauling grounds) in New Zealand, with peak numbers following the breeding season (Crawley and Wilson 1976). The maximum number of *A. forsteri* at Macquarie Island is concurrent with that for the whole population of fur seals there (Fig. 5).

Population size

The index of abundance used by Csordas and Ingham (1965) and by Johnstone (1972) is the maximum annual count of all animals on North Head Peninsula between mid-February and early April. These counts have been made when and where most of the seals occur and when most of those ashore are *A. forsteri*. The appropriate figure for the population size in 1981-82 (Fig. 6) is 861 animals.

The trend in the index of abundance from 1949-50 (when the first counts were made) to 1981-82 (Fig. 6) indicates that the population has been gradually increasing. For the whole island, the count has increased from 176 seals in early 1950 to 1,222 in March 1982. The variability of annual counts can be attributed to several causes: they have been carried out by a series of observers; they were made after the breeding season, primarily of nonbreeding animals that had no ties to land; and, in some years, only a single count was made.

Food

The only published information concerning food is for four animals of unknown specific identity (Csordas and Ingham 1965). They were probably *A. forsteri*, since no remarks were made on their pelage color, and they were collected when seals of the *A. gazella/A. tropicalis* group were rarely reported. Squid beaks, fish bones and scales, and penguin feathers and bones were identified in their stomachs. Squid and fish remains were not identified to species. Seal scats also contained penguin feathers. They were thought to be from rockhopper and royal penguins *Eudyptes crestatus* and *E. schlegeli*, the two most numerous species at Macquarie Island. Two other penguins (king, *Aptenodytes patagonicus*; and gentoo, *Pygoscelis papua*) occur at Macquarie Island. The former was considered to be too large to be prey for fur seals and the latter too few to support many predators. In addition, these authors noted that penguin skins were not infrequently washed ashore during January-March when fur seals were plentiful.

Unidentified fur seals at Macquarie Island have been recorded feeding on seabirds on two occasions. On 19 March 1973 a fur seal chased, caught, and ate a royal penguin in the sea near the Nuggets. On 14 June 1977 a fur seal was seen flinging a blue-eyed cormorant *Phalacrocorax atriceps* about on the surface off the Isthmus. This is recognized as feeding behavior in other fur seals, e.g., *A. p. pusillus* (Rand 1959).

In New Zealand waters *A. forsteri* feeds primarily on squid, *Loligo* spp.; octopus, *Octopus* spp.; and barracouta, *Leionura atun* (Street 1964), whereas at subantarctic Campbell Island principal foods are squid and rockhopper penguin (Bailey and Sorensen 1962).

STATUS AND BIOLOGY OF *A. GAZELLA/ A. TROPICALIS* AT MACQUARIE

Spatial distribution

Almost all the *A. gazella/A. tropicalis* group occurs on the east coast of North Head Peninsula. In the 1981-82 and 1982-83 summers a few were seen at the northern extremity of the peninsula, but the majority occurred on two bays: Secluded Beach and the southern end of Goat Bay. Pups were born on these two bays only. Csordas and Ingham (1965) reported pups at these localities from 1954-55 to 1963-64; they referred to the latter as Fur Seal Coves. Habitat in these bays is similar to the intermediate type in Bester's (1982) classification for *A. tropicalis* at Gough Island, with small boulders and a few large rocks.

In the March 1982 census, the only other place where these seals were sighted was Hurd Point (Table 1). One (a pup) was seen at Brothers Point in March 1976. In March 1984, 15 were seen at Handspike Point and 1 at Hurd Point (G. Copson, Natl. Parks Wildl. Serv., Tasmania, pers. commun.). A pup may have been born at Hurd Point in April 1957 (Csordas and Ingham 1965).

Temporal distribution

Numbers of the *A. gazella/A. tropicalis* group ashore are highest in January (Fig. 5). Few were ashore during the 1982 winter. This group is in the minority at the island, except possibly in early December soon after fur seals begin arriving and their numbers increase more rapidly than those of *A. forsteri*.

Population size

Information on trends in population size is available from three sources. First, counts of animals during the breeding season showed a small increase from 1981-82 to 1982-83. For this comparison, four age/sex classes were used: bulls (which were holding territories); subadult males (recognized by their creamy-colored chest and face, smaller size, but not holding territories); cows (which may have included young animals of either sex); and black pups. In 1981-82, numbers in these four classes were 3, 1, 15, and 15, respectively, whereas in 1982-83 they were 5, 2, 30, and 20. Both counts were made by the same observer, but the increase may be partly caused by more thorough searches and greater experience in species identification in the second season.

Second, counts of pups born at Macquarie between 1954-55 and 1983-84 (Table 2) show an increase which has been most marked

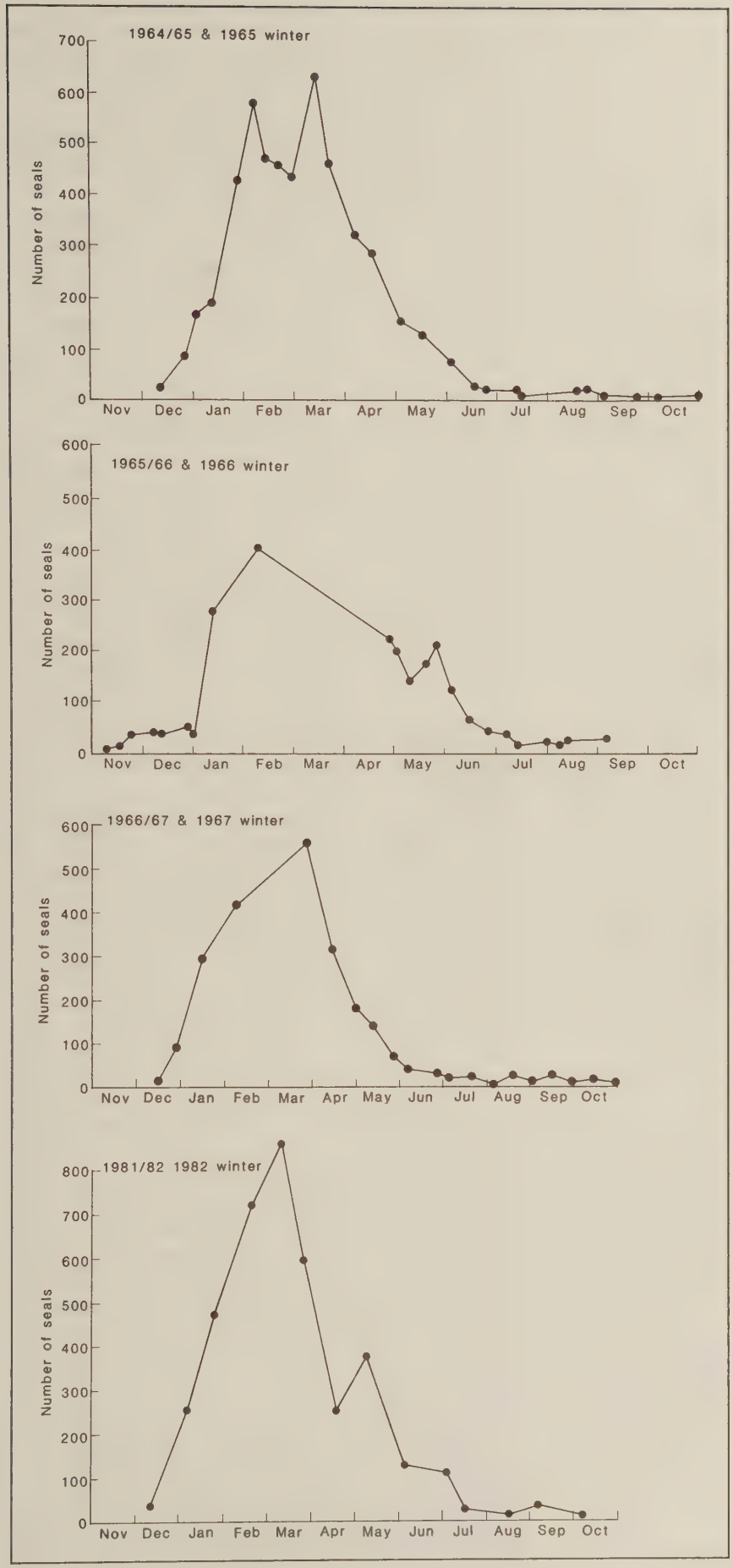

1964/65 & 1965 winter
1965/66 & 1966 winter
1966/67 & 1967 winter
1981/82 1982 winter
Number of seals
Nov Dec Jan Feb Mar Apr May Jun Jul Aug Sep Oct

Figure 4—Annual variation in counts of all fur seals on North Head Peninsula, Macquarie Island.

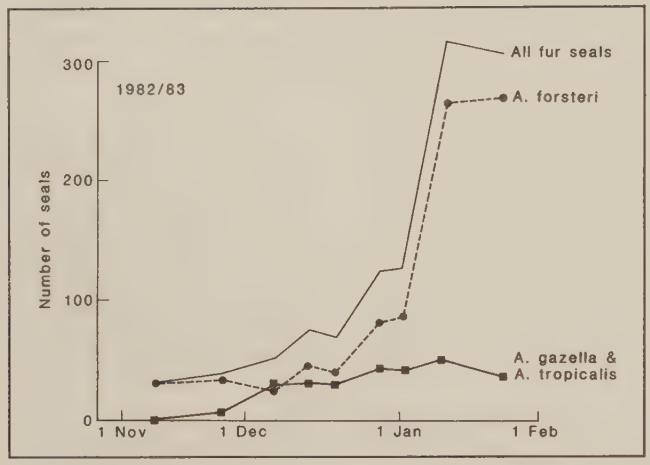


Figure 5—Variation in counts of *A. forsteri* and *A. gazella*/*A. tropicalis* on North Head Peninsula, Macquarie Island, summer 1982-83.

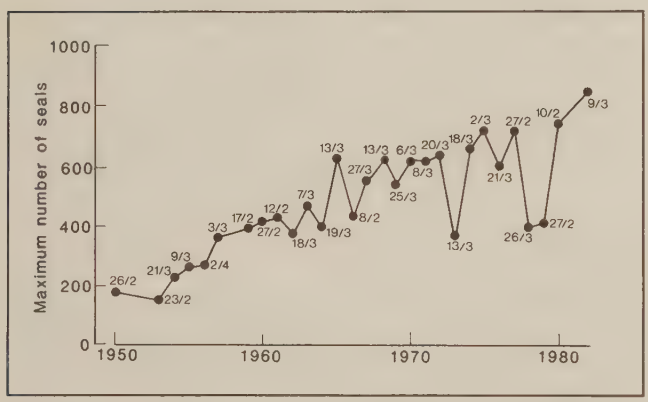


Figure 6—Maximum annual counts of fur seals on North Head Peninsula, Macquarie Island, 1950-1982, showing day and month. Counts of all fur seals in February, March, or early April when numbers were near maximum. [Data from Csordas and Ingham (1965); Johnstone (1972); ANARE station fur seal logbooks; 1981 count by Fletcher].

Table 2—Timing of pupping and number of fur seal pups of the *A. gazella*/*A. tropicalis* group recorded at North Head Peninsula, Macquarie Island[a].

Year	Inspection from mid-Nov.	First pup seen	Max. numbers recorded	Comments
1954-55	—[b]	7 March	1[c]	
1955-56	5 Dec.	8 Dec.	2 by 26 Feb.[c,d]	
1956-57	—	5 Dec.	1[c,d]	2-3 days old
1957-58	—	30 Nov.	1[c]	Placenta attached
1958-59	Dec.		0[c]	
1959-60	Dec.		0[c]	
1960-61	—	18 Dec.	1	
1961-62	—	24 March	1	Dead pup
1962-63	28 Feb.	—	0[c]	
1963-64	22 Jan.	5 Feb.	1[c]	
1964-65	11 Dec.	26 Dec.	4 by 28 Jan.[c]	
1965-66	16, 23 Nov.			
	8, 11 Dec.	26 Dec.	3 by 18 Feb.[c]	
1966-67	None	16 Dec.	2 by 26 Dec.[c]	
1967-68	25 Nov.	12 Dec.	4 on 9 Jan.[c]	
1968-69	16, 29 Nov.	9 Dec.	3 on 30 Dec.[c]	
1969-70	15 Dec.	18 Dec.	1	
1970-71	26 Nov.			
	14 Dec.		0 on 8 March	
1971-72	None		0 on 16 Jan.	Goat Bay only
1972-73	None		0 on 13 March	
1973-74	None		0 on 18 March	
1974-75	None	25 Dec.	2 on 2 March	
1975-76	None	29 Dec.	6 on 29 Dec[c]	Includes 1 dead pup; another live pup at Brothers Pt. 12 March
1976-77	None	17 Dec.	4 on 27 Feb.	
1977-78	None	—	—	
1978-79	None	—	0 on 27 Feb.	
1979-80	None	4 Dec.	9 on 10 Feb.	
1980-81	7 Dec.	14 Dec.	6 on 24 Dec.	Goat Bay only
1981-82	None	1 Dec	15 on 9 March[c]	13 seen by 19 Dec.
1982-83	12 Nov.	26 Nov.	20 on 12 Jan.[c]	Includes 2 dead pups; 14 recorded by 14 Dec.
1983-84	None	2 Dec.	19 on 16 Jan.[c]	

[a]Data for 1954-55 to 1963-64 from Csordas and Ingham (1965).
[b]Dash indicates no information available.
[c]Thorough search made.
[d]Evidence obtained for the presence of a (or another) pup.
[e]Csordas (1958).

since 1981-82. These counts have been carried out by many observers, which must account for some of their variability.

A third, less precise indication is the scarcity of reports of the easily recognizable *A. tropicalis* males until 1981-82.

Pupping period

The earliest date that a pup was recorded was 26 November 1982 (Table 2). In several years maximum pup numbers were not recorded until much later. We believe this does not result from an extended pupping season, but from the scarcity of visits to pupping sites and the difficulty of finding pups in the caves and rocky terrain they inhabit. Based mostly on the observations made in 1955-56 to 1957-58, 1966-67 to 1969-70, 1976-77, 1979-80, and 1981-82 to 1983-84, it appears that pups are born from late November to mid-December.

Mortality

Information on pup mortality was available for two summers when searching was thorough. In 1982-83, 2 of the 20 pups were found dead by age 1 month. In 1975-76, seven pups were found, one of which was dead. Therefore pup mortality rate to age 1 month is 11%. This is likely to be an underestimate, as dead pups are more likely to have been overlooked than live ones.

Degree of polygyny

Counts of bulls, cows, and pups in the territories (reported above) provide overall ratios of five cows and five pups per bull in 1981-82; for 1982-83 the ratios are six cows and four pups per bull. The maximum number of cows in a territory was 12. That territory contained a subadult male that was tolerated by the bull. For territories with a single male, the maximum number of cows was eight.

Lactation

At Marion and Gough Islands, Kerley (1983a) and Bester (1981) reported that weaning in *A. tropicalis* was a gradual process which began in late September and in mid-August, respectively. Information on departure dates (Table 3) indicates that 6 of the 33 pups conform to the known weaning dates of *A. tropicalis*. Without close observation the cessation of suckling and departure of a pup will rarely be observed. Two pups at Macquarie Island received such scrutiny. During the winter of 1967, coves containing pups bearing tags numbered 5 (female) and 6 (male) were visited approximately fortnightly from late March to 3 August, daily or twice daily until 5 September, and fortnightly again until the next season's pups were born. Pup 5 was last seen on 29 September, but was absent on the next (15 October) and subsequent visits. Pup 6 was last seen on 18 August.

Arctocephalus gazella pups at Marion Island are reported to wean from late March, with a median date of 28 March (Kerley 1983a). Only three pups at Macquarie Island were last seen at about that date, all in 1976 (Table 3). They were ashore on 21 March but not seen during later searches on 7 June and 29 July. They may have been *A. gazella* pups and weaned successfully, or they may have died. On the basis of weaning dates for *A. gazella* and *A. tropicalis* at Marion Island, other pups at Macquarie Island last seen ashore in January, February, and May-July (Table 3) are unlikely to have weaned successfully.

Data are available on the attendance patterns of cows to two tagged *A. tropicalis* pups in 1967 (nos. 5 and 6) up to their departure. Pup 5 was attended by a cow on 10 of 41 days (25%) on which it was inspected to 29 September, whereas pup 6 was attended by a cow on 2 of 30 days (6.7%) to 18 August. The frequency of attendance by cows to early February was significantly greater than that from the end of March when observations resumed (Fisher exact probability tests, $P=0.037$ and $P=0.014$, respectively).

During an intensive period of daily or twice-daily inspections between 3 August and 5 September, a cow was with pup 5 on two occasions, each of which spanned 2 days. The first visit lasted for 1 to 2.1 days, the second for 1.2 to at least 2.2 days. They were separated by 9 days.

Growth

Pup weights at age 3 to 5 weeks are available for a total of 11 animals from two summers, 1975-76 and 1981-82. For four males the mean weight is 7.2 kg with standard error of the mean 1.34 and range 5.0 to 8.6. Seven females weighed 6.4±1.48 kg, range 4.0 to 9.2.

Information on the growth rate of pups is available for four tagged pups (one male, three females) over 83 days in the summer of 1975-76, from 29 December to 21 March. In that period their average weight increased from 5.4 to 10.7 kg, with a mean growth rate of 0.066 kg/day. One (a female) was weighed again on 7 June. For the 78 days from March to June its weight increased from 11.0 to 15.5 kg, at a mean growth rate of 0.058 kg/day.

For 1967, information is available on the growth rate of two pups from 31 March. The data for a female (tag 5) cover 171 days to 18 September (i.e., from age 4 to 9½ mo approximately); those for a male (tag 6) cover 113 days to 22 July (4 to 8 mo). The female pup increased from 10.4 to 16.8 kg by 22 July, at an average daily rate of 0.040 kg/day and then decreased to 12.7 kg by 18 September. It was last seen on 29 September. The male pup increased from 11.1 to 13.9 kg by 19 May, at an average daily rate of 0.036 kg/day and then decreased to 10.9 kg by 22 July. It was last seen on 18 August. Both pups decreased in weight for the same length of time before leaving the island, namely 8 weeks. Weight losses were 24% and 21%, respectively, of the maximum recorded weights.

Table 3—Duration of time spent ashore by fur seal pups of the *A. gazella* and *A. tropicalis* group at North Head Peninsula, Macquarie Island.

Year	Max pup nos.	Pups marked[f]	Pups last seen	Later checks to mid-Nov.	Last check
1954-55[a]	1	No	29 May	None recorded	—[a]
1955-56[a]	2	No	11 and 26 Feb.	5	End May
1956-57[a]	1	No	18 May	1	30 May
1963-64	1	Yes	10 Feb.	3	19 March
1964-65	4	Yes	14 Feb., 3 June (2), 12 July[b]	9	16 Nov.
1965-66	3	Yes	8 Feb. (2), 31 July	3	6 Sep.
1966-67	2	Yes[d,g]	18 Aug., 29 Sep.	3	11 Nov.
1967-68	4	Yes (for 3)	9 Jan., 14 Feb., 27[b] and 29 Sep.	4	16 Nov.
1968-69	3	Yes	7 June, 14 and 24 Sep.	3	28 Oct.
1969-70	1	Yes[d]	8 March	7	25 Aug.
1975-76	6[e]	Yes[h]	29 Feb., 21 March (3), 29 July	None	
1981-82	15	No	5 June (6), 6 Sep. (2)[c]	3	12 Nov.

[a]Data from Csordas and Ingham (1965); S. E. Csordas checked regularly during 1955 and 1957 winters.
[b]Pup with cow.
[c]Last date not determined for other pups.
[d]Juveniles also tagged, 3 in 1966-67 and 1 in 1969-70.
[e]Includes one dead pup (not tagged).
[f]Monel metal tags.
[g]Also hot iron branded, in July.
[h]Yellow, numbered plastic tags also applied.

Food

Stomach contents of an adult male *A. tropicalis* at Macquarie Island were collected by J. K. Ling in March 1963 (S. Aust. Mus., Adelaide, pers. commun. 19 April 1984). The food items consisted of partly digested squid 15-20 cm long.

INCIDENTAL OBSERVATIONS

Young fur seals (22 pups and 4 juveniles) have been tagged on the fore-flipper with numbered, monel-metal or yellow plastic tags in eight summers (Table 3). Three have been resighted after their first year, all at the island (Table 4). The largest interval between tagging and resighting was a little over 9 years, for an *A. forsteri* juvenile (no. 8) tagged in April 1967. Of the three resightings, this seal was at the greatest distance from the tagging site (10 km).

Only one fur seal at the island has been recorded carrying a man-made object other than a flipper tag. It was a young animal of unknown species with a blue collar on its neck seen on the eastern side of North Head Peninsula on 6 January 1974. Collars of artificial fiber have been reported on *A. gazella* at South Georgia (Payne 1979; Bonner and McCann 1982), but not on *A. tropicalis* or *A. forsteri*.

One of the seven cows in Goat Bay on 19 December 1981 was heavily infested on its hindquarters with barnacles. From its pelage coloration the cow was identified as one of the *A. gazella*/*A. tropicalis* group. The barnacles were not inspected since the cow

Table 4—Resightings of tagged fur seals at Macquarie Island after their first year.

Tagging data						Resighting data			
Date	Age class	Sex	Species[a]	Location	Tag no.	Date	Age (years)	Location	Minimum distance (km)
18 April 67	Juvenile	M	*A. forsteri*	Goat Bay	8	6 June 76	10½	Brothers Pt.	10
10 Feb. 76	Pup	—[b]	*A. gazella/ A. tropicalis*	Goat Bay or Secluded Beach	Y[c]	23 Dec. 79	4	Secluded Beach	0
22 March 70	Juvenile	F	*A. gazella*	Hasselborough Bay	20	16 Feb. 71	2+	Langdon Pt.	4.5

[a]Pup belongs to the *A. gazella/A. tropicalis* group; for juveniles identification was based on description of pelage coloration and, for the 1970 one, inspection of a transparency by G. W. Johnstone (Antarct. Div., Hobart).
[b]Dash indicates no information available.
[c]Yellow plastic tag.

could not be caught. It was not seen again. Barnacles have been reported on *A. gazella* at South Georgia (Bonner 1968) and on *A. forsteri* in South Australia (Stirling 1971).

DISCUSSION

At Macquarie Island *A. tropicalis* bulls, and cows of both *A. tropicalis* and *A. gazella*, were present in the 1981-82 and 1982-83 breeding seasons. Evidence is provided that pups of both species also occurred then. As bulls, cows, and pups of *A. tropicalis* occur at the island, it seems likely that this species mates and pups there and so should be added to the list of mammals breeding in Australia. Bulls of *A. gazella* have not been sighted, so we cannot be sure that this species breeds at the island.

The situation at Macquarie Island of *A. gazella* and *A. tropicalis* hauling out together is not unique, as it occurs at Marion Island (Condy 1978; Kerley 1983a,b) and Iles Crozet (Jouventin et al. 1982). Likewise, the apparent interbreeding of the two species at Macquarie Island, as evidenced by *A. tropicalis* bulls holding territories containing cows and pups suspected of being *A. gazella* and *A. tropicalis*, is paralleled at the other islands, where hybrids of the two species have been reported and suspected.

Space does not appear to limit population growth of fur seals at Macquarie Island, as much of the shoreline of the east coast (which appears to be preferred to the west coast) is uninhabited. Even though both groups occupy mainly rocky shores on North Head Peninsula, they do not appear to be competing for space since the peninsula's coastline is not densely utilized, even when maximum numbers are ashore. If the population continues to increase, it is possible that competition for space may become important, especially on North Head Peninsula.

Arctocephalus tropicalis might be expected to haul out at Heard Island and Iles Kerguelen, which are both located between Macquarie and the other islands this species inhabits, but no evidence for this has been found. The species has not been mentioned in recent reports of fur seals at Kerguelen reviewed by Jouventin et al. (1982). At Heard Island in January and February 1983, members of the Heard Island Expedition 1983 searched most beaches and bays, at the request of the senior author, but saw no *A. tropicalis* (Vining 1983). *Arctocephalus gazella* breeds at both localities.

The *A. gazella/A. tropicalis* population at Macquarie Island is of similar size now to that of *A. gazella* at South Georgia in the 1930s (Bonner 1968) and those of *A. tropicalis* at Marion and Gough Islands before the 1950s (Rand *in* Condy 1978; Swales *in* Bester 1980). The number of pups born at Macquarie Island appears to have increased in recent years, but the breeding population does not yet seem to be expanding rapidly in the manner of those at South Georgia, Marion, and Gough Islands. Although the dynamics of these increases have been studied, their early stages were not well documented, particularly from the point of view of social organization. It seems surprising that these populations did not increase more rapidly at an earlier date, and the extent to which social and topographical factors may have been restrictive would make a particularly interesting study, for which the Macquarie Island population might well be suitable.

At Macquarie Island attempts should be made to identify all cows in breeding territories; to determine if *A. gazella* bulls occur at the island and within breeding territories; to determine if mating occurs among the *A. gazella/A. tropicalis* group and, if so, whether it occurs within each species and between the species; to determine if *A. forsteri* is involved in mating or pupping; to expand on the methods currently available for distinguishing between pups of the three species which occur there; to determine if pups are born at sites other than the east coast of North Head Peninsula; to determine the fate of pups; to determine feeding habits from scats, and determine the identity of animals producing individual scats; and to collect blood samples from cows and pups for determination of transferrin type to assist in their identification.

Solutions to the identification problems outlined in the previous paragraph would be aided if better descriptions of the species involved were available from their breeding localities. In particular, the following would be helpful.

(1) Tape recordings and sonograms of calls of *A. tropicalis* and of hybrids of that species and *A. gazella*, to complement sonograms in Stirling and Warneke (1971).

(2) Better descriptions of pups of the three species; e.g., shapes of the head and snout and presence or absence of muzzle coloration should be checked in series of pups. In addition, the ratio of foreflipper and hindflipper lengths to standard length should be determined for pups of each species; these characters were used to distinguish between small seals of *A. gazella*, *A. tropicalis*, and *A. p. pusillus* by Shaughnessy and Ross (1980).

As this information becomes available, it will be possible to predict more reliably whether the fur seal population at Macquarie Island is likely to expand markedly from increments resulting from breeding occurring there, or to continue increasing slowly as a result of immigration only.

ACKNOWLEDGMENTS

Much of the information reported here has been collected by expeditioners to Macquarie Island. We thank all of them, and in particular W. D. McKenzie, J. Dart, P. J. Ormay, G. W. Johnstone, and E. Jones. Permission to consult fur seal log books was provided by the Antarctic Division. D. Rounsevell, S. Cronin, D. Montgomery, N. Brothers, and G. Copson of the National Parks and Wildlife Service, Tasmania, also provided assistance.

R. Carrick, S. E. Ingham, and G. W. Johnstone provided advice and encouragement which resulted in many observations being recorded in fur seal log books at the ANARE Station. S. E. Ingham, G. W. Johnstone, J. P. Croxall, G. L. Shaughnessy, and W. N. Bonner provided constructive criticism on a draft of this report.

G. I. H. Kerley, W. N. Bonner, D. W. Doidge, and R. H. Mattlin examined photographs of seals and assisted in their identification. D. Parer recorded vocalizations of seals. R. Tomkins and the ABC-TV Film Library provided the tape and videotape recordings. P. J. Fullagar and F. Knight produced sonograms of the tape recordings and the figures, respectively.

Assistance with tracing specimens and old records was provided by L. Gibson (Australian Museum, Sydney), J. M. Dixon (Museum of Victoria, Melbourne), A. N. Baker (National Museum of New Zealand, Wellington), J. K. Ling (South Australian Museum, Adelaide), and F. Jacka (Mawson Institute for Antarctic Research).

CITATIONS

BAILEY, A. M., and J. H. SORENSEN.
1962. Subantarctic Campbell Island. Proc. Denver Mus. Nat. Hist. 10:1-305.

BESTER, M. N.
1980. Population increase in the Amsterdam Island fur seal *Arctocephalus tropicalis* at Gough Island. S. Afr. J. Zool. 15:229-234.
1981. Seasonal changes in the population composition of the fur seal *Arctocephalus tropicalis* at Gough Island. S. Afr. J. Wildl. Res. 11:49-55.
1982. Distribution, habitat selection and colony types of the Amsterdam Island fur seal *Arctocephalus tropicalis* at Gough Island. J. Zool. (Lond.) 196:217-231.

BONNER, W. N.
1968. The fur seal of South Georgia. Br. Antarct. Surv. Sci. Rep. 56:1-81.

BONNER, W. N., and T. S. McCANN.
1982. Neck collars on fur seals, *Arctocephalus gazella*, at South Georgia. Br. Antarct. Surv. Bull. 57:73-77.

CARRICK, R.
1957. The wildlife of Macquarie Island. Aust. Mus. Mag. 12:255-260.

CONDY, P. R.
1978. Distribution, abundance, and annual cycle of fur seals (*Arctocephalus* spp.) on the Prince Edward Islands. S. Afr. J. Wildl. Res. 8:159-168.

CRAWLEY, M. C., and R. WARNEKE.
1979. New Zealand fur seal. *In* Mammals in the seas, p. 45-48. FAO Fish. Ser. 5, vol. 2.

CRAWLEY, M. C., and G. J. WILSON.
1976. The natural history and behaviour of the New Zealand fur seal (*Arctocephalus forsteri*). Tuatara 22:1-29.

CROWTHER, W. L.
1933. Macquarie Island and its animal life. Emu 33:14-17.

CSORDAS, S. E.
1958. Breeding of the fur seal, *Arctocephalus forsteri* Lesson, at Macquarie Island. Aust. J. Sci. 21:87.
1962. The Kerguelen fur seal on Macquarie Island. Victorian Nat. 79:226-229.
1963. The history of fur seals on Macquarie Island. Victorian Nat. 80:255-258.

CSORDAS, S. E., and S. E. INGHAM.
1965. The New Zealand fur seal, *Arctocephalus forsteri* (Lesson), at Macquarie Island, 1949-64. CSIRO Wildl. Res. 10:83-99.

CUMPSTON, J. S.
1968. Macquarie Island. ANARE (Aust. Nat. Anarct. Res. Exped.) Sci. Rep. Ser. A(1), 380 p.
1974. Kangaroo Island 1830-1836. Roebuck, Canberra, 218 p.

DEBENHAM, F. (editor)
1945. The voyage of Captain Bellingshausen to the Antarctic Seas, 1819-21. [Engl. transl.] The Hakluyt Society, London, 2 vols.

FALLA, R. A.
1962. Exploitation of seals, whales and penguins in New Zealand. Proc. N.Z. Ecol. Soc. 9:34-38.
1965. Birds and mammals of the subantarctic islands. Proc. N.Z. Ecol. Soc. 12:63-68.

GRENFELL PRICE, A.
1962. The winning of Australian Antarctica: Mawson's B.A.N.Z.A.R.E. Voyages 1929-31. BANZARE (Br. Aust. N.Z. Antarct. Res. Exped.) 1929-31 Sci. Rep. A 1, 241 p.

GWYNN, A. M.
1953. Notes on the fur seals at Macquarie Island and Heard Island. ANARE (Aust. Nat. Antarct. Res. Exped.) Interim Rep. 4:1-16.

HAINSWORTH, D. R.
1972. The Sydney traders. Simeon Lord and his contemporaries 1788-1821. Cassell, Melbourne, 264 p.

JOHNSTONE, G. W.
1972. A review of biological research by Australian National Antarctic Research Expeditions, 1947-71. Polar Rec. 16:519-532.

JOUVENTIN, P., J. C. STAHL, and H. WEIMERSKIRCH.
1982. La recolonisation des Iles Crozet par les otaries (*Arctocephalus tropicalis* et *A. gazella*) [Recolonization of the Crozet Islands by the *Arctocephalus tropicalis* and *A. gazella* fur seals]. Mammalia 46:505-514.

KERLEY, G. I. H.
1983a. Comparison of seasonal haul-out patterns of fur seals *Arctocephalus tropicalis* and *A. gazella* on subantarctic Marion Island. S. Afr. J. Wildl. Res. 13:71-77.
1983b. Relative population sizes and trends, and hybridization of fur seals *Arctocephalus tropicalis* and *A. gazella* at the Prince Edward Islands, Southern Ocean. S. Afr. J. Zool. 18:388-392.
1984. Relationships between sympatric breeding populations of fur seals (*Arctocephalus* sp.) at Prince Edward Islands. S. Afr. J. Sci. 80:28-29.

LESSON, R.-P.
1828. Phoque. *In* J. B. G. M. Bory de Saint-Vincent (ed.), Dictionnaire classique d'histoire naturelle, vol. 13, p. 400-426. Rey et Gravier, Paris.

McNAB, R.
1909. Murihiku and the southern islands. Auckland, Wilson and Horton (reprinted 1970). Whitcombe and Tombs, Wellington, 377 p.
1913. The old whaling days; A history of southern New Zealand from 1830 to 1840. Golden Press, Auckland (reprinted 1975), 508 p.

MAWSON, D.
1915. The home of the blizzard. Heinemann, London, 2 vols.
1923. Macquarie Island and its future. Pap. Proc. R. Soc. Tasmania 1922:40-53.
1940. Marine biological programme and other zoological and botanical activities. Australas. Antarct. Exped. 1911-14 Sci. Rep. A 2(5):127-167.
1942. Geographical narrative and cartography. Australas. Antarct. Exped. 1911-14 Sci. Rep. A 1:1-364.
1943. Macquarie Island, its geography and geology. Australas. Antarct. Exped. 1911-14 Sci. Rep. A 5:1-194.

PAYNE, M. R.
1979. Fur seals *Arctocephalus tropicalis* and *A. gazella* crossing the Antarctic Convergence at South Georgia. Mammalia 43:93-98.

RAND, R. W.
1959. The Cape fur seal (*Arctocephalus pusillus*). Distribution, abundance and feeding habits off the southwestern coast of the Cape Province. S. Afr. Div. Sea Fish. Invest. Rep. 34:1-75.

REPENNING, C. A., R. S. PETERSON, and C. L. HUBBS.
1971. Contributions to the systematics of the southern fur seals, with particular reference to the Juan Fernandez and Guadalupe species. *In* W. H. Burt (ed.), Antarctic Pinnipedia. Antarct. Res. Ser. 18:1-34.

SHAUGHNESSY, P. D.
1970. Serum protein variation in southern fur seals, *Arctocephalus* spp., in relation to their taxonomy. Aust. J. Zool. 18:331-343.
1982. The status of the Amsterdam Island fur seal. *In* Mammals in the seas, p. 411-421. FAO Fish. Ser. 5, vol. 4.

SHAUGHNESSY, P. D., and G. J. B. ROSS.
1980. Records of the Subantarctic fur seal (*Arctocephalus tropicalis*) from South Africa with notes on its biology and some observations on captive animals. Ann. S. Afr. Mus. 82:71-89.

STIRLING, I.
1971. Studies on the behaviour of the South Australian fur seal, *Arctocephalus forsteri* (Lesson) II. Adult females and pups. Aust. J. Zool. 19:267-273.
STIRLING, I., and R. M. WARNEKE.
1971. Implications of a comparison of the airborne vocalizations and some aspects of the behaviour of the two Australian fur seals, *Arctocephalus* spp., on the evolution and present taxonomy of the genus. Aust. J. Zool. 19:227-241.
STREET, R. J.
1964. Feeding habits of the New Zealand fur seal *Arctocephalus forsteri*. N.Z. Mar. Dep., Fish. Tech. Rep. 9:1-20.
TAYLOR, R. H.
1969. Fur seals at Antipodes Islands 1969. *In* J. H. Sorenson (ed.), New Zealand fur seals with special reference to the 1946 open season. N.Z. Mar. Dep., Fish. Tech. Rep. 42:79-80.
1979. Seals at the Bounty and Antipodes Islands. Unpubl. rep., Ecology Div., DSIR, Nelson, N.Z., 13 p.
VINING, R.
1983. Search for Subantarctic fur seals. p. 28, *In* R. Vining (ed.), Heard Island Expedition 1983 Scientific Reports. Sydney, Aust. 55 p.

Recolonization Processes in the Subantarctic Fur Seal, *Arctocephalus tropicalis*, on Amsterdam Island

JEAN-PAUL ROUX[1]
Institut des Sciences de l'Evolution
Section Socio-Ecologie
USTL Place Bataillon
34060 Montpellier Cedex
France

ABSTRACT

Uncontrolled sealing during the 18th and 19th centuries brought the Amsterdam Island population of *Arctocephalus tropicalis* to the brink of extinction. The numerical and geographical recovery has been studied since 1956. Changes in the rate of increase and in the extension of the breeding sites demonstrate the processes of recolonization of the island. Successive phases are described and compared with other *Arctocephalus* population recoveries.

INTRODUCTION

Saint Paul and Amsterdam Islands are less than 100 km apart and situated in the Indian Ocean, midway between southern Africa and Australia. The great abundance of subantarctic fur seals, *Arctocephalus tropicalis*, on these islands was noted as early as the first landings by van Vlaming in 1696 and Silo in 1754 (Paulian 1964). Uncontrolled and indiscriminate exploitation of the fur seal population started soon after these first visits, e.g., the *Mercury* and the *Britannia* voyages in 1789 and 1791, respectively. During this time, seals were very heavily culled since at least eight different vessels are known to have sealed on these islands between 1792 and 1796 (De Brossard 1971; Paulian 1964).

After 1842, occasional and opportunistic harvesting by whalers and fishermen was still occurring. The last recorded sealing operation was in 1874 (De Brossard 1971). According to 19th century authors Studer and Goodenough (Paulian 1964), fur seals had already become rare and later were believed to be extinct on both islands (Aubert de la Rue 1932; Jeannel 1940). However, a nucleus of seals must have remained on a remote part of the coast, probably on Amsterdam Island which was the least visited of the two. The west coast is the most likely since it is nearly inaccessible and is known to have been the site of the first breeding colonies established by 1952.

NUMERICAL RECOVERY

Since the seals were rediscovered, censuses of the Amsterdam Island population have been carried out by means of direct counts during the breeding season (from December to March) along the entire coastline in 1956 (Paulian 1964), 1970 (Segonzac 1972), and 1982 (Roux 1982; Hes and Roux 1983). The results of these are presented in Figure 1, together with the 1972 estimates which were obtained by means of counts and capture-recapture experiments on pups (Tollu 1974). The total figures take into account only the seals present on the island during one breeding season. Therefore they are not total population estimates since, for example, the yearlings which have completely left the coast by the end of October (Roux and Hes 1984) are not included.

Seal numbers have increased 15-fold in 26 years (1956-82). The overall mean annual rate of increase, calculated from total numbers of 1956 and 1982 censuses, is 10.4% which is close to the annual rate of increase in pup production of 11.8% during the same period. The rate of increase of the population (the slope of the fitted curve in Fig. 1) has changed considerably during this time and has increased by two to three times between 1956-70 and 1970-82 (Table 1).

It seems unlikely that immigration from other subpopulations has had an important effect during this recolonization since all the other breeding localities of *A. tropicalis* were recolonized during the same period or later: Gough Island (Bester 1980), Tristan da Cunha (Bester 1980), Marion and Prince Edward Islands (Rand 1956; Condy 1978), Saint Paul Island (Segonzac 1972), and the Crozet Group (Jouventin et al. 1982).

GEOGRAPHICAL RECOVERY

It is highly probable that seals were breeding almost everywhere along the coastline prior to exploitation. During recolonization, the extension of the breeding colonies was monitored (Fig. 2). In 1956,

[1]Present address: Sea-Fisheries, P.O. Box 394, 9000 Lüderitz, S.W.A./Namibia.

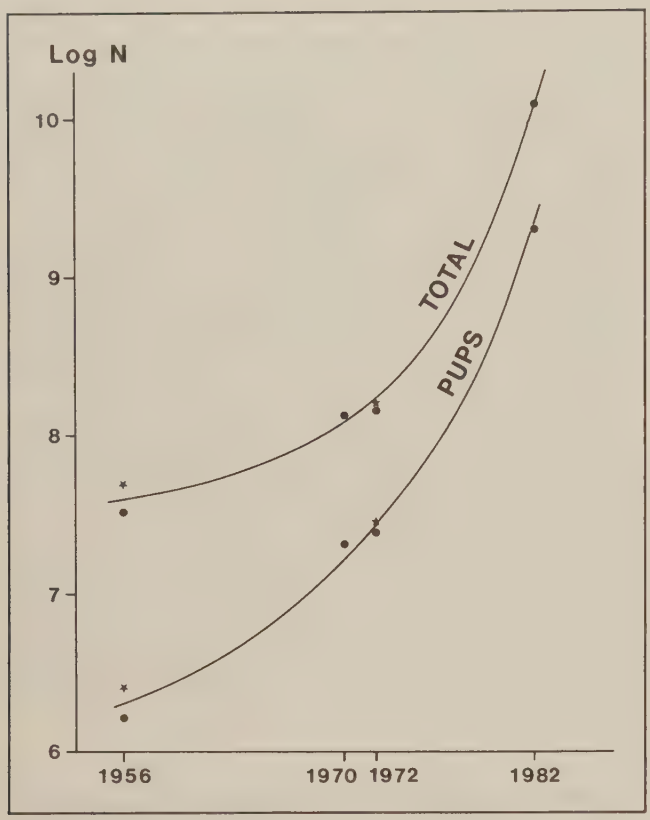


Figure 1—Numerical increase of the Amsterdam Island fur seal.

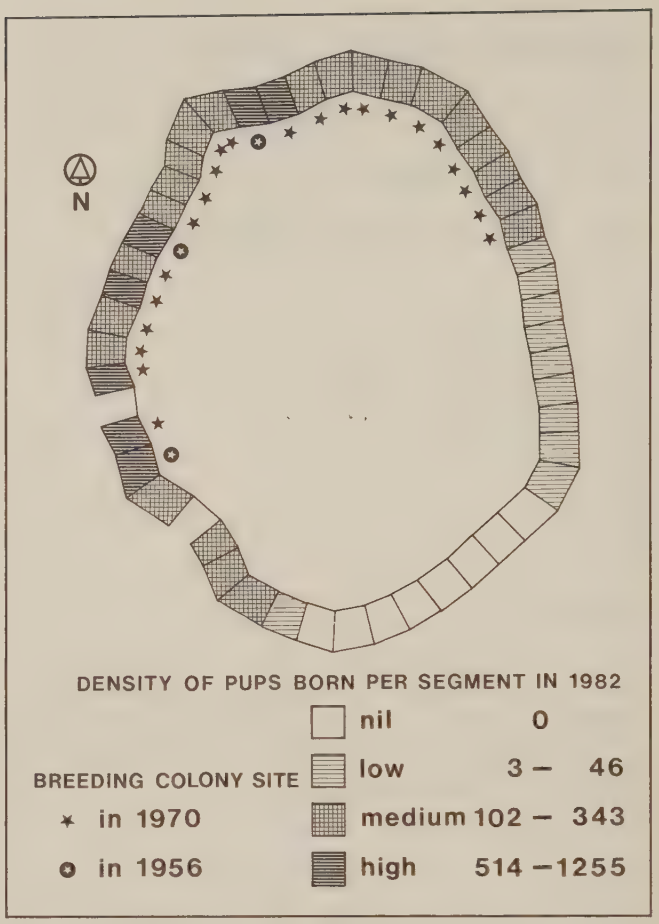


Figure 2—Map of Amsterdam Island coastline showing density of *A. tropicalis* pups born per segment in 1982 and location of the breeding colonies in 1956, 1970, and 1982.

Table 1—Observed rates of population increase of *A. tropicalis* on Amsterdam I. calculated from census data.

	Annual rate of increase	
Period	Total population	Pup production
1956-70	5.3%	7.9%
1970-82	16.4%	16.6%

only three small breeding colonies, occupying 6.1% of the coastline, existed and were situated on the west coast. The extension of these original colonies resulted in the occupation of 48.9% of the coastline by breeding seals in 1970 and 81% of the coastline in 1982.

It is likely that fur seals will soon occupy as much as 96% of the coastline. The remaining 4% is not suitable since it lacks hauling-out sites.

NUMERICAL DISTRIBUTION

For the 1982 census (Hes and Roux 1983) the coastline was divided into 49 segments 570+20 m in length, and the number of seals per segment was used as a density index. Figures 3a and b show the total number of fur seals and the number of pups, respectively. The latter count is a better measure of the breeding population. Differences in the environmental factors (e.g., available space, type, and size of rocks) between the various segments are insufficient to explain the present density distribution (Roux unpubl. data).

Density is much higher on the sites of the original three breeding colonies of 1956 (segments 32, 40, and 46). In 1982, 30% of the births occurred on these three sites (representing only 6% of the coastline), and 52% occurred within one segment on either side of these original sites (representing 18% of the coastline). Similarly, the lowest densities are found on the most recently colonized sections of the island and, overall, there is a significant correlation between the number of pups born in each segment and the establishment dates of the breeding colonies ($r=0.76$, $N=39$, $p<0.01$; Fig. 4).

Hes and Roux (1983) noted that an initial rapid rate of increase, up to 28% per year, occurred on the newly colonized sections. For the northern sector (3 segments colonized between 1956 and 1970) and for the eastern and southern sectors (24 segments colonized after 1970), the initial annual rates of increase were 20.8% and 28%, respectively, for total numbers, and 25.3% and 27.1% for pups. Between 10 and 15 years after the establishment of breeding, the local rate of increase on such sites has decreased to half its previous value, as illustrated in Figure 5 for three segments of the north coast. This phenomenon and the present density distribution suggest that overflow from previously established high-density breeding colonies to adjacent beaches is the major process of geographical recolonization.

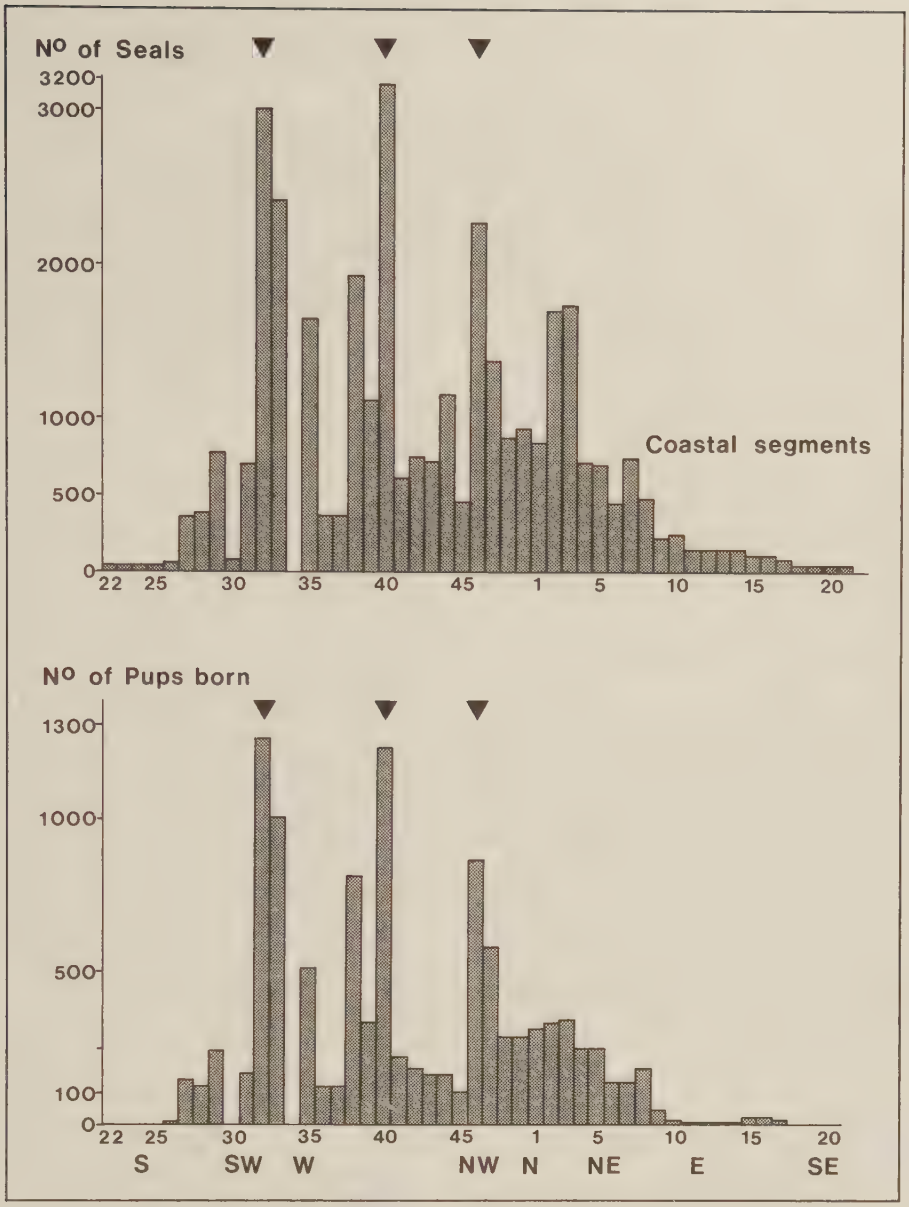


Figure 3—Fur seal distribution during the peak in numbers (December 1981) along the Amsterdam Island coastline, divided into 49 segments. Solid triangles show locations of the three original breeding colonies found in 1956.

RECOLONIZATION PHASES

Although recolonization has been a continuous phenomenon since exploitation ceased, it can be divided into four successive phases according to changes in the rate of increase (Roux 1982), the spatial distribution (Hes and Roux 1983), and the density.

Phase I: Survival

Seal numbers were reduced to an extremely low level, and reproductive activities were disturbed and probably disrupted by indiscriminate overexploitation. The survival phase lasted from the cessation of sealing (circa 1880) to the establishment of the first breeding colonies (probably after 1930). It is characterized by extremely low densities and few breeding individuals. According to the level of the population in 1956, the rate of increase during this period must have been minimal (less than 5% per year). This implies a much lower breeding success during Phase I than presently. Hunting activities might have modified the age-group distribution and possibly the sex ratio to such an extent that the optimal social structure could not be attained. In addition, the potential breeding animals that survived might have been too dispersed along the coastline to allow efficient reproduction.

Phase II: Establishment

This phase is characterized by the establishment of a few breeding colonies (e.g., three for Amsterdam Island). The annual rate of increase is lower than 10%, increasing as the density increases. Pup mortality seems to decrease as the density changes from low to medium. Indeed, males only hold territories along the shoreline under low-density conditions, and therefore most pups are born in

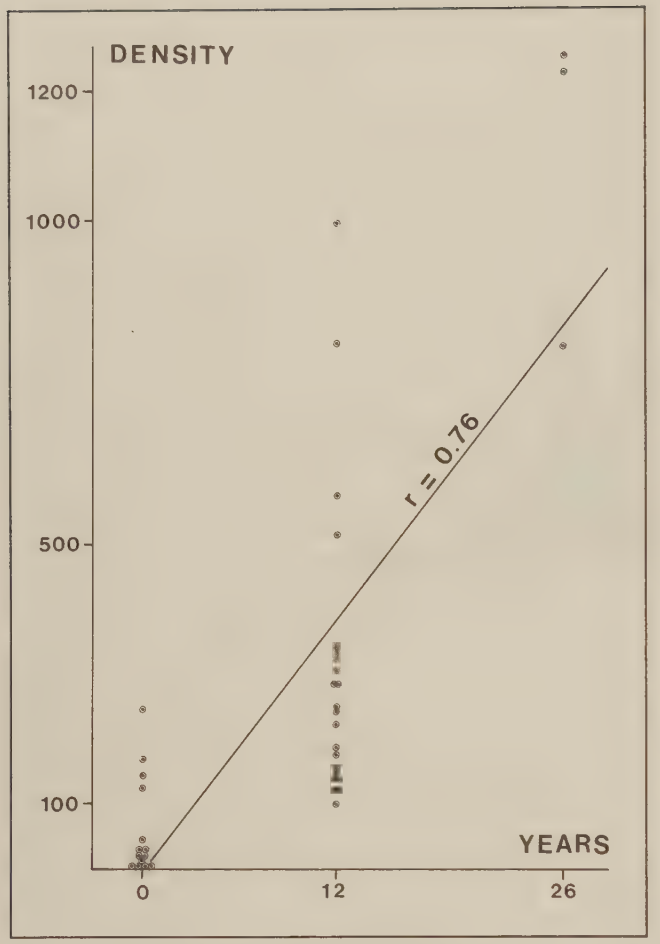


Figure 4—Relationship between number of *A. tropicalis* pups born per segment and minimum age of the breeding colonies.

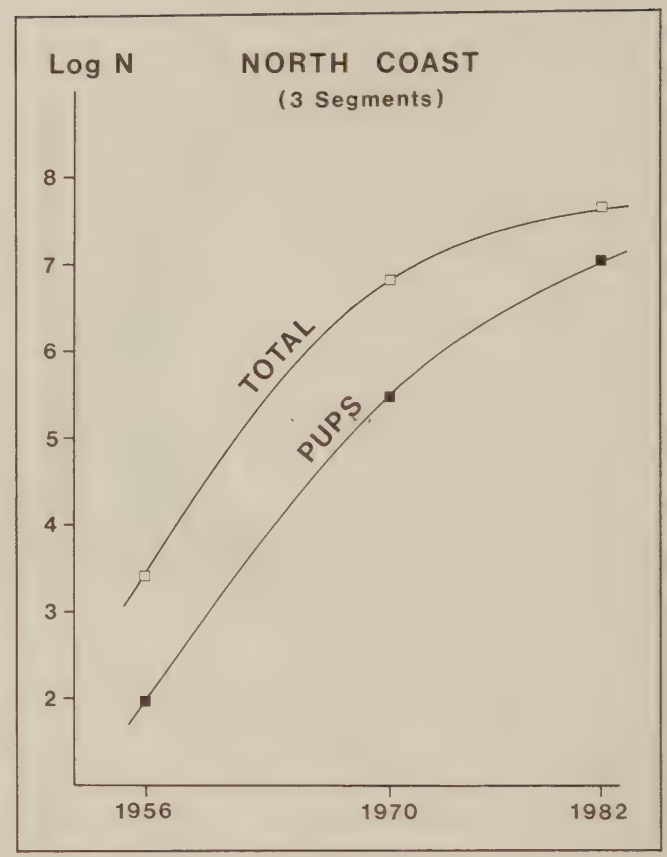


Figure 5—Changes in numbers of *A. tropicalis* in the north coast subpopulation between 1956 and 1982.

the vicinity of the waterline. Thus, during the first 2 weeks after birth, a high proportion of the pup mortality is caused by the sea (Paulian 1964; Tollu 1974). This proportion may increase substantially in the event of a storm, as was the case in 1956 when 47% of the total pup population died within 3 weeks (Paulian 1964). As density increases, the males utilize the entire beach area. Therefore the proportion of all pups exposed to these elements decreases and the impact of storms becomes far less severe, e.g., 14% pup mortality in their first 12 weeks, despite two storms just after the peak in births in a medium-density colony (Hes and Roux 1983). In 1956 the Amsterdam Island population was at the end of the establishment phase.

Phase III: Recolonization

When density reaches high values on the original breeding colonies, shortage of space during the breeding season initiates a local emigration towards the available sites nearby. Consequently, a rapid recolonization of the coastline occurs. These emigrants are probably young animals since adults remain faithful to their breeding sites.

During this phase, the rate of increase for the total population can attain 15-17% per year. For Amsterdam Island, Phase III started after 1956 and is still in progress. The duration of this phase is dependent on the size of the remaining sites suitable for breeding.

Phase IV: Maturity

When density reaches high values on all sites suitable for breeding (or in the case of a large island, when the total population becomes too high compared with the amount of available food), density-dependent factors (space shortage, food shortage, etc.) tend to stabilize the population size and structure. From the evolution of high-density established colonies, a drop in the rate of increase can be expected during this phase.

DISCUSSION

The recolonization pattern observed on Amsterdam Island closely resembles that of other recolonizing *Arctocephalus* populations, suggesting that the processes are similar.

On Gough Island, the *A. tropicalis* population annually increased by 8.9% before 1955 and then by 15.9% between 1955-56 and 1977-78 (Bester 1980) when a large extension of the breeding colony sites occurred (Bester 1977). This population was therefore presumably in Phase III before 1977. But according to Bester (1980) the optimum breeding space is becoming limited, indicating the onset of Phase IV, during which a drop in the rate of increase is expected.

On the Crozet Islands (Ile de la Possession), the *A. tropicalis* population appears to be in Phase II since only a single breeding

colony is established. The increase in numbers in this colony, and thus the increase in density (Jouventin et al. 1982), indicates that Phase III may begin soon.

On the Prince Edward Islands the *A. tropicalis* population's rate of increase was 10.5% between 1952 and 1975 (Condy 1978) and 15.0% between 1975 and 1982 (Kerley 1983). Furthermore, a large extension of the colony sites in the vicinity of previously colonized beaches) had occurred (Kerley 1983). These changes are characteristic of Phase III. Some of the newly colonized sites (e.g., Cliff Beach, Cape Davis and Triegaardt Bay) show local rates of increase over 20% (i.e., 21% and 27%; Kerley 1983), similar to the newly colonized sites of Amsterdam Island.

In South Georgia the first breeding colonies of *A. gazella* were found in 1936 after cessation of sealing. These were situated on the Willis Islands and Bird Island. The extremely high annual rate of increase observed on the latter, 27.1% and 22.1% between 1956 and 1958 (Bonner 1964), suggests the occurrence of immigration from previously colonized sites (Willis Islands?). The drop in the rate of increase of the Bird Island subpopulation, observed between 1959 and 1963 (Bonner 1964, 1968), might correspond to Phase IV. Payne (1977) suggested that this drop in the observed rate of increase might be due to undercount. More recent data (Doidge et al. 1984) indicate a very low rate of increase for the Bird Island colonies, showing that an actual drop in the growth rate of this subpopulation has occurred. However, on the mainland some breeding colonies were established by 1961-62 in the vicinity of Bird Island (Bonner 1964, 1968). Since then, further increases in numbers and distribution have occurred on the mainland (Laws 1973; Payne 1977, 1978; Doidge et al. 1984) with a 16.8% annual rate of increase, which suggests that the South Georgia population, as a whole, is still in Phase III.

Similarly, the Kerguelen population, as a whole, is entering recolonization Phase III, since some established breeding colonies on the mainland (west coast) have been found in 1984. Immigration from the high-density colony on Iles Nuageuses (Jouventin et al. 1982) is certainly still occurring.

On Amsterdam Island the present rate of increase of 16.5% per year is high but not exceptional for southern fur seals. It is similar to other recolonizing populations of *A. tropicalis*: 15.9% on Gough Island (Bester 1980), 15.0% on Marion and Prince Edward (Kerley 1983); and of *A. gazella*: 16.8% on South Georgia (Payne 1977). A closed population of southern fur seals seems able to sustain a maximum rate of increase of 15-17% per year during recolonization. However, very high rates of increase have been observed on some colonies: 25.3% and 27.1% (Hes and Roux 1983); 27.1% and 22.1% (Bonner 1964); 38% (Doidge et al. 1984); 20.9% and 27.2% (Kerley 1983), due to local immigration during recolonization Phase III. These localized effects invalidate estimates of population increase when based on partial counts as long as a detailed history of recolonization is unknown.

During recolonization, the annual rate of increase (r) has undergone great variations: $r < 5\%$ in Phase I, $5\% < r < 10\%$ in Phase II, and $15\% \leqslant r$ in Phase III. These variations seem to be a general phenomenon as they appear in other expanding *Arctocephalus* populations. Such variations in the rate of increase (in any population) must be due to variations in demographic parameters like fecundity, survivorship, age at maturity, or age distribution. As suggested earlier, at least pup survival seems to vary in a complex density-dependent scheme, increasing as density changes from low to medium and then decreasing only when density reaches high values.

Under these conditions, it is understandable that the lower the numbers (after cessation of sealing), the longer the duration of Phase I. Thus, such effects could explain the delay between the cessation of sealing and the attainment of high rate of increase during recolonization (Phase III). The *A. tropicalis* recolonization pattern suggests that the effect of density-dependent factors is delayed in comparison with the logistic model, a certain minimum density being necessary for the attainment of the maximum rate of increase, agreeing therefore with the view of Fowler (1981) that density dependence in the dynamics of large mammals is generally nonlinear.

These hypotheses are consistent with data on other recolonizing *Arctocephalus* populations (Bester 1980; Bonner 1968; Condy 1978; Doidge et al. 1984; Kerley 1983). These are also consistent with the concept of a threshold density in population models for seals (De Master 1981) and the suggestion of a leptokurtic yield curve, i.e., producing highest yields near maximal population levels (Eberhardt and Siniff 1977), or the concentration of density-dependent change at high population levels for large mammals and particularly marine mammals (Fowler 1981).

ACKNOWLEDGMENTS

This work was a contribution to the program "Ecologie des Oiseaux et Mammifères Antarctiques" (Ecology of Antarctic Birds and Mammals) of Terres Australes et Antarctiques Francaises (TAAF) and RCP764 of CNRS, under the scientific direction of P. Jouventin. It was part of a cooperative research program between TAAF and the Mammal Research Institute, University of Pretoria. We would like to express our sincere thanks to the Director of MRI, Professor J. D. Skinner, to A. D. Hes for his help, and the 32nd and 33rd relief teams to Amsterdam Island for their hospitality. We would also like to acknowledge J. P. Gleeson for his encouragement before his untimely death through an accident in the field. Thanks are also due to J. P. Croxall, C. W. Fowler, and T. S. McCann for helpful comments on the manuscript.

CITATIONS

AUBERT de la RUE, E.
1932. La faune des îles Saint-Paul et Amsterdam (Fauna of the Saint Paul and Amsterdam Islands). Terre Vie 11:642-662.

BESTER, M. N.
1977. Habitat selection, seasonal population changes and behaviour of the Amsterdam Island fur seal *Arctocephalus tropicalis* on Gough Island. D Sc. Thesis, Univ. Pretoria, R.S.A., 193 p.
1980. Population increase in the Amsterdam Island fur seal *Arctocephalus tropicalis* at Gough Island. S. Afr. J. Zool. 15:229-234.

BONNER, W. N.
1964. Population increase in the fur seal *Arctocephalus tropicalis gazella* at South Georgia. *In* Carrick, R., J. Prevost, and M. W Holdgate (eds.), Proc. 1st SCAR Symp. on Antarctic Biology, p. 433-443. Paris.
1968. The fur seal of South Georgia. Br. Antarct. Surv. Sci. Rep. 56, 93 p.

CONDY, P. R.
1978. Distribution, abundance and annual cycle of fur seals (*Arctocephalus* spp.) on the Prince-Edward Islands. S. Afr. J. Wildl. Res. 8:156-168.

DeBROSSARD, M.
1971. Kerguelen, le découvreur et ses îles (Kerguelen, the explorer and his islands). 2, Iles australes. France Empire, Paris, 541 p.

DeMASTER, D. P.
1981. Incorporation of density dependence and harvest into a general population model for seals. *In* Fowler, C. W. and T. D. Smith (eds.), Dynamics of large mammals populations, p. 389-401. John Wiley and Sons, New York.

DOIDGE, D. W., J. P. CROXALL, and J. R. BAKER.
1984. Density-dependent pup mortality in the Antarctic fur seal *Arctocephalus gazella* at South Georgia. J. Zool. (Lond.) 202:449-460.
EBERHARDT, L. L., and D. B. SINIFF.
1977. Population dynamics and marine mammals management policies. J. Fish. Res. Board Can. 34:183-190.
FOWLER, C. W.
1981. Density dependence as related to life history strategy. Ecology 62:602-610.
HES, A. D., and J-P. ROUX.
1983. Population increase in the subantarctic fur seal *Arctocephalus tropicalis* at Amsterdam Island. S. Afr. J. Antarct. Res. 13:29-34.
JEANNEL, R.
1940. Au seuil de l'Antarctique (On the threshold of the Antarctic). Mus. Nat. Hist. Nat., Publ. 5, Paris, 236 p.
JOUVENTIN, P., J-C. STAHL, and H. WEIMERSKIRCH.
1982. La recolonisation des îles Crozet par les otaries *Arctocephalus tropicalis* et *A. gazella* (Recolonization of the Crozet Islands by the fur seals, *Arctocephalus tropicalis* and *A. gazella*). Mammalia 46:505-514.
KERLEY, G. I. H.
1983. Relative population sizes, trends and hybridization of fur seals *Arctocephalus tropicalis* et *A. gazella* at the Prince Edward Islands, Southern Ocean. S. Afr. J. Zool. 18:388-392.
LAWS, R. M.
1973. Population increase of fur seals at South-Georgia. Polar Rec. 16:856-858.
PAULIAN, P.
1964. Contribution à l'étude de l'otarie de l'île Amsterdam (A contribution to the study of the Amsterdam Island fur seals). Mammalia 28:1-146.
PAYNE, M. R.
1977. Growth of a fur seal populaiton. Philos. Trans. R. Soc. Lond. B 279:67-79.
1978. Population size and age determination in Antarctic fur seal *Arctocephalus gazella*. Mammal Rev. 8:67-73.
RAND, R. W.
1956. Notes on the Marion Island fur seal. Proc. Zool. Soc. Lond. 126:65-82.
ROUX, J-P.
1982. L'otarie d'Amsterdam (The Amsterdam Island fur seal). Actes du VI^{e} Colloq. de Mammalogie, La Rochelle :75-79.
ROUX, J-P., and A. D. HES.
1984. The seasonal haul-out cycle of the fur seal *Arctocephalus tropicalis* (Gray, 1872) on Amsterdam Island. Mammalia 48:377-389.
SEGONZAC, M.
1972. Données récentes sur la faune des îles Saint-Paul et Nouvelle Amsterdam (Recent data on the fauna of Saint Paul and New Amsterdam Islands). Oiseau Rev. Fr. Ornithol. 42:3-68.
TOLLU, B.
1974. L'otarie de l'île Amsterdam (The Amsterdam Island fur seal), *Arctocephalus tropicalis tropicalis* (Gray, 1872). These de doctorat de 3eme cycle, Paris, TAAF, 88 p.

Behavior of Fur Seals

FRITZ TRILLMICH, Rapporteur
Max-Planck-Institut für Verhaltensphysiologie
Abteilung Wickler
D-8131 Seewiesen
W. Germany

The species summaries in this volume show how much comparative information on fur seal behavior has recently become available. Although a large amount of descriptive work that still needs to be done, particularly for the little-studied *Arctocephalus* species, it seems timely to try and push the analysis one step further by asking questions about the influences of social, environmental, and physiological parameters on the behavior of individuals. In this session, three behavioral complexes basic to the social organization of Otariids were discussed: female gregariousness, male territoriality, and the regulation of the feeding-nursing cycle of females. The female feeding-nursing cycle has already been discussed and was treated briefly in the session on female attendance.

FEMALE GREGARIOUSNESS

Female density greatly influences the degree of polygyny realized in a fur seal species. There are three—not mutually exclusive—hypotheses that could conceivably account for female gregariousness.

The best known hypothesis, called the "marginal male effect" (Bartholomew 1970), assumes that males' survival abilities and physical vigor are to some extent heritable. Females can thus derive genetic benefits from breeding with the most physically fit males. Female gregariousness increases male-male competition and thus insures that only the strongest males will have access to them (Cox and LeBoeuf 1977). Although additive genetic variance of fitness traits theoretically should soon be exhausted under strong selection, this may not be the case in large populations living in fluctuating environments.

An "ecological marginal male effect" (Trillmich and Trillmich 1984) can take two forms: (1) High female density may decrease the intensity and frequency of male-female interactions, thus reducing any dangers to a female's health that may result from the frequent aggressive male/female interactions; and (2) gregariousness may reduce the danger of attacks by subadult males on a given pup either through a selfish herd effect (Hamilton 1971) (i.e., by decreasing the probability that a given pup will be attacked by an intruding male), and/or through the exclusion of subadult males from pupping areas by territorial males.

No data relevant to the marginal male effect have been collected. Circumstantial evidence suggests that an ecological marginal male effect may be operative in several species. In *Callorhinus ursinus*, a territorial male has much more control of a single female on a territory than of a single female in a group of females. In *Otaria byronia*, subadult males are frequently observed attacking and often killing pups. Thus, male behavior may be a major determinant of female gregariousness. Presumably, the positive correlation between density and pup mortality eventually stops the selection for ever-increasing female gregariousness.

TERRITORIAL BEHAVIOR

Males of all fur seal species have very similar behavior patterns. Striking differences in territorial tenure, number of fights per unit time, and degree of polygyny achieved appear to depend on the social and physical environment. Female density and the synchrony of pupping are the most important social factors in male territorial behaviors. This can be seen when the subpolar and tropical species

are compared. For the subpolar species which have high female density and very synchronized breeding seasons, territorial tenure can be readily seen, but becomes much less clear in the Galapagos fur seal or the Galapagos sea lion where males may be on territory twice within one season, and may even leave their territory repeatedly for feeding during "tenure." The structure of the habitat influences male territory position and size partly by governing female distribution and partly by setting the constraints for thermoregulation on land.

Considering this multitude of influences, males must be flexible in their behavior patterns. The conditions for, and the amount of, this flexibility are almost unstudied. One way to learn more about these aspects of male behavior would be to measure the costs and benefits of various actions on the reproductive success of bulls. Fur seals are ideal subjects for such studies, as copulations can be counted and provide a fairly good measure of reproductive success. A few unanswered questions show how accessible this field is to detailed study: How do weight differences influence the outcome of a fight? Do wounds influence fighting success? What are the consequences of a serious wound on subsequent territorial behavior of a male and on his prospects for further territory tenure?

MATERNAL BEHAVIOR

Rates of energy flow from the environment to the mother, and from mother to pup, appear to play a decisive role in determining the length of the nursing-foraging cycle of females with pups.

Experiments of Gentry et al. (1986) on Northern fur seals have shown that the rate of energy transfer from mother to pup determines the duration of the female's presence on land. It is unclear if the rate of milk synthesis limits the rate of energy transfer as we do not know how much preformed milk exists in the mammary gland when the female arrives ashore and how much is synthesized when the female is on land. Milk production, more likely sets the lower limit on the duration of visits ashore. The rate of energy transfer increases strongly with the age of the pup (Costa and Gentry 1986).

Data about energy gain during foraging trips suggest that females forage until they have replenished their fat reserves (Costa and Gentry 1986). The presence ashore of a pup does not seem to influence their return decision very much. When food availability was low, female South American fur seals stayed at sea far longer than normal, apparently trying to bring their fat reserves back to the normal physiological upper set-point. Many stayed out too long and lost their pups (Trillmich et al. 1986).

CITATIONS

BARTHOLOMEW, G. A.
1970. A model for the evolution of pinniped polygyny. Evolution 24:546-559.

COSTA, D. P., and R. L. GENTRY.
1986. Free ranging and reproductive energetics of the Northern fur seal. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur seals: Maternal strategies on land and at sea. p. 79-101. Princeton Univ. Press, Princeton, N.J.

COX, C. R., and B. J. LeBOEUF.
1977. Female incitation of male competition: a mechanism of mate selection. Am. Nat. 111:317-335.

GENTRY, R. L., G. L. KOOYMAN, and M. E. GOEBEL.
1986. Feeding and diving behavior of Northern fur seals. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur seals: Maternal strategies on land and at sea, p. 61-78. Princeton Univ. Press, Princeton, N.J.

HAMILTON, W. D.
1971. Geometry for the selfish herd. J. Theor. Biol. 31:295-311.

TRILLMICH, F., G. L. KOOYMAN, P. MAJLUF, and M. SANCHEZ-GRIÑAN.
1986. Attendance and diving behavior of the South American fur seal during "El Niño" in 1983. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur Seals: Maternal strategies on land and at sea, p. 153-167. Princeton Univ. Press, Princeton, N.J.

TRILLMICH, F., and K. G. K. TRILLMICH.
1984. The mating systems of pinnipeds and marine iguanas: convergent evolution of polygyny. Biol. J. Linn. Soc. 21:209-216.

Male Fur Seal Tenure

T. SEAMUS McCANN, Rapporteur
British Antarctic Survey
Natural Environment Research Council
High Cross, Madingley Road
Cambridge CB3 0ET
United Kingdom

The session on male tenure was concerned with the period spent ashore by adult males during the breeding season, in particular when males are defending a territory. Discussion concentrated on the factors affecting male tenure within a season and from year to year and the consequences of tenure, rather than the details of the activities occurring in the territories.

In all species the vast majority of copulations are performed by tenured males. Without a territory in a place frequented by females, and the ability to defend it, a male will have virtually no access to estrous females.

In the subpolar species (Antarctic and northern fur seals) a great influx of adult males to the breeding grounds starts 2-3 weeks before the females haul out and continues throughout the period of pupping and mating. But in tropical and temperate species, adult males can be found ashore throughout the year and the onset of tenure is perhaps more difficult to define. Tenure can range from less than one day to more than 60 days, can cover the whole season of pupping and mating, or even take place exclusively before or after mating has occurred.

A number of factors, which are extensively interrelated, affect duration of tenure. These include age, size, ability to fast, ability to fight, climate, access to water for thermoregulation, territory location, distribution of females, and population density.

Young males (less than 7 years old in *Arctocephalus gazella*) are too small to fight successfully with adult males. The smaller size of younger males also affects their ability to fast. Across species, however, the relationship between body size and fasting ability is not necessarily straightforward. Thus, the maximum period of tenure recorded for several species of fur seal (*Callorhinus ursinus*, *A. gazella*, *A. australis*, *A. forsteri*) is similar (60-70 days) despite large differences in average adult body size. Maximum period of tenure exceeds the length of the mating period, but because prime males tend to return to sea when there are no more estrous females available (thus ceasing tenure), maximum recorded tenure may be more directly related to the duration of the breeding season than to fasting ability. At present there are insufficient data on the energetics of fasting in territorial males to clarify the relationship between size, body reserves, and period of tenure.

In old *C. ursinus* males, both body weight and number of copulations decline. Whether these changes occur because tenure is shorter in these old males is unclear. The oldest harem males in a sample of *A. gazella* were 11 years, although other males are known to survive to at least 13 years. Either these older males fail to achieve tenure or else they defend territories in marginal areas.

Tenure in a season was generally shorter in *A. gazella* males that had shoreline territories because competition was greater in areas which attracted the largest numbers of females. Conversely, copulation frequency was greater in these areas because males with shoreline territories did not have to abandon their territory for thermoregulation. This was also true of *A. forsteri*. The mean period of tenure for *A. gazella* males that copulated was twice as long as for those that did not, but in both *C. ursinus* and *A. pusillus* some males have held tenure for long periods in poor areas and have not achieved any copulations.

In *A. forsteri*, the earliest males to acquire territories are younger ones and these give way to later arriving older males who acquire the preferred sites (those with shade and water). In *A. pusillus* and *C. ursinus* younger males tend to gain territories later, after the prime males have weakened or departed. Six years of data on known *C. ursinus* males at San Miguel Island show that as males get older they come ashore earlier and acquire territories in better areas. Site fidelity

seems to be highly developed in *C. ursinus* and *A. pusillus*, and males are known to return to the same areas in successive seasons, even if they have not been successful in that area because of lack of females. Those at San Miguel may be less site-specific. It is not known whether there is any relationship between site specificity in females and site fidelity in territorial males. The extent of movement of territory site between seasons and of changes in tenure and reproductive success are unstudied in most species.

The relative advantages to lifetime reproductive success of attempting to acquire territory early or late in life, and of arriving on-site early or late in the breeding season, are important concepts which require extensive study, especially in view of the considerable inter- and intraspecific variation that is likely to exist. Males that come ashore early can probably gain a territory more easily than later arriving ones, but they will have used up more of their reserves by the time the greatest number of females are in estrus, thus they might be at a disadvantage relative to males who deferred their arrival. The available data suggest that males tend to come ashore earlier in successive seasons. However, the costs and benefits of different strategies for males of different size and age have not yet been quantified.

Population density is known to affect territory size in *A. gazella*, with territories being smaller in areas of greater density. It is not known whether territory size also affects the duration of tenure, but this seems possible because greater competition has been shown to result in a faster turnover of males who are in favored positions.

The costs of tenure have not been estimated. These include the physiological costs of fasting, the extreme exertion of fighting, and the cost of sustaining wounds. Most territorial males bear numerous cuts gained in fights; occasionally these are extensive or seriously debilitating. Even apparently small wounds can become seriously infected and mortality of *A. gazella* ashore is considerably greater in socially mature males than in subadults.

Female Fur Seal Attendance Behavior

T. SEAMUS McCANN, Rapporteur
British Antarctic Survey
Natural Environment Research Council
High Cross, Madingley Road
Cambridge CB3 0ET
United Kingdom

COW ATTENDANCE STUDIES

The session on adult female attendance behavior was divided into two parts: patterns of shore attendance, and activities while ashore. The former included the time and duration of the pupping season; the number of days the female stayed ashore around parturition; duration of subsequent absences from shore for feeding and of visits ashore to nurse the pup; changes in the patterns of attendance over the lactation period; and length of the lactation period (the period of dependence of the pup). Activities ashore included perinatal activities, suckling patterns and alien suckling (suckling of nonfilial pups), activity budgets, and site fidelity.

Patterns of shore attendance

Studies of attendance behavior have been carried out to (1) establish patterns of shore use by females to elucidate details of the annual cycle, (2) compare different breeding locations, (3) correlate patterns of tooth structure, and (4) examine the feasibility of using attendance patterns as an indicator of food availability and environmental change.

The time of pupping, annual cycle, and length of the lactation period are broadly known for all fur seal species. The extent of synchrony of pupping is less well known, but differences appear to be related to the seasonality of the environment, with *Arctocephalus gazella* and *Callorhinus ursinus* having the shortest pupping seasons and *A. galapagoensis* the longest. Despite this difference, some species (e.g., *A. forsteri* in New Zealand) have a very short season in an environment of relatively low seasonality. Information on breeding synchrony in the literature is often difficult to compare (Table 1). The period during which the middle 90% of births occurred should be used to describe pupping synchrony and is best characterised using a simplified Probit analysis (Caughley 1977) on the census data.

For most fur seals the length of the perinatal attendance period is approximately 7 days, although it varies between individuals from about 3 to 12 days. The reasons for this variation are unknown, although condition of the female may be important. Perinatal attendance in *A. gazella* was shorter in a year of food shortage.

Feeding trip length increased as lactation progressed in *C. ursinus*, whereas in *A. galapagoensis* trip duration did not change but trip frequency did. Both changes were probably a response to increased demand by the pup. Analysis of seasonal change in trip length should not be made by calendar date because variations in birth date may mask such seasonal changes (e.g., in *C. ursinus* records). Analysis should be made by trip number or time after birth. No changes in mean trip length were observed in *C. ursinus* over a period of 30 years despite the development of a major commercial fishery in the seals' summer feeding area. However, *A. gazella* at South Georgia has shown considerable year-to-year variation in feeding trip length which may reflect changes in the availability of the major food resource at this time.

The need to identify individuals is fundamental to the problem of investigating patterns of attendance. Paint and bleach make good marks on cows and pups, but tags are the best permanent markers. Some of the more recent cattle ear tags are proving durable and readable after several years, but a desire was expressed for a tag designed especially for seals, although this would probably be costly. Telemetry has been used successfully on *C. ursinus* and *A. gazella*, providing information on exact arrival and departure times and also on possible foraging area in *A. gazella*. Transmitters can be glued to the fur using epoxy resin or attached to a harness. Transmitters

Table 1—Female fur seal attendance patterns.

	Female migration	Age at weaning (months)	Pupping synchrony—90% of births (weeks)	% of days female available to pup	Feeding trips		Fasting female		Attend. duration (days)	Time of maximum attendance
					No.	Mean length (days)	Arrival to parturition (days)	Parturition to 1st trip (days)		
Callorhinus ursinus	+	4	3-4	27	8-12	6.9	1.2	8.3	2.1	Day
Arctocephalus gazella	+	4	3	36	14-19	4.3	1.8	6.9	2.1	Day
A. pusillus	–	9-11	4-5	39	50-60	2.9	1.5	4.3	2.4	Day
A. australis (Peru)	–?	12-24	10	(27)	?	4.7*	?	?	1.3	Day
A. australis (Uruguay)	–	8-12	—	—	—	—	—	—	—	—
A. galapagensis	–	18-36	10	c 40	300	1.5	1.5	7.3	0.5-1.3	Day
Zalophus c. wollbaeki	–	10-12*	16-40	73	200	0.5	1.5	6.8	0.6	Night
A. forsteri	–	10	4	—	—	1-5	2.1	c 0.9	2-4	—
A. philippii	–	—	—	—	—	—	—	—	—	—
A. tropicalis	–	9-11	4-6	—	—	—	—	—	—	—
A. townsendi	–	9-11	6	—	—	—	—	—	—	—

*In an El Niño season.

glued to the head remained attached for 6-14 weeks. Care must be taken in positioning receivers to avoid interference and bounce-back from topographical features; chart recorders need regular observation and maintenance.

Onshore activities

Seventy percent of onshore pup mortality in *A. gazella* occurs in pups younger than 7 days old (and 50% within 2 days of birth), i.e., during the perinatal attendance period. Failure of the mother-pup bond to form, with subsequent trauma and starvation of the pup, is thought to be the principal cause of mortality. The successful establishment of the mother-pup bond is crucial to survival. Quantitative data on its formation and the subsequent history of pups are lacking. It would be valuable to observe females of known age and breeding history, and in particular to compare primiparae with multiparae.

The relationship between time spent suckling and amount of milk transferred has been studied in some species. In *A. galapagoensis* the correlation between these two factors is very weak; yearlings suck for a shorter time than pups but get much more milk. Weight gain is the best measure of milk transfer and suckling time seems to be a poor estimate of this, although in conjunction with other measures it can be useful, e.g., as a measure of pup effort. Alien suckling appears to occur at a very low frequency in most species. It is seen frequently in *A. gazella* on high-density beaches but its importance is not known. Pups do not need a stable relationship (i.e., adoption) with a cow in order to benefit from alien suckling but this requires more detailed investigation.

Some species have particular requirements for suckling and resting sites. *A. galapagoensis* requires shade for thermoregulation, and suitable sites are limited. Large females displace smaller ones from favoured sites. Space is less important in other species where access to shade or water for cooling is more abundant. Activity budgets have been investigated in very few species to date. Their principal value is to compare different species or populations, or to illustrate changes in activity or time allocation over a given period. Females do not spend all their time ashore with the pup or looking for it. Experiments on *A. gazella* using telemetered animals have shown that some females move away from the suckling site after having attended the pup, but do not go to sea. Some had alternative suckling sites. Telemetry, supported by visual checks, is the best way of following activities in species such as *A. gazella*, which often make considerable movements while ashore; however, telemetry is not required for following species such as *C. ursinus* which move over short distances while on shore.

Site fidelity varies between species. *C. ursinus* is very site-specific both in terms of place of pupping in consecutive seasons and in suckling site within a season. Other species are less site-specific though this varies considerably, both within and between species. In some, e.g., *A. australis* in Peru, haul-out sites are limited, resulting in limited movement of females. It is not known whether variations in site fidelity are related to population density, rookery substrate (movement by *A. gazella* away from areas which become progressively muddier), or a species-specific tendency to move. *A. tropicalis* and *A. gazella* both show great variation in site specificity in a season, with females of *A. gazella* frequently moving hundreds of meters inland to suckle their pups. Both of these species have a tendency to establish new breeding sites on widely dispersed islands.

CITATION

CAUGHLEY, C.
1977. Analysis of vertebrate populations. John Wiley and Sons, New York.

Fur Seal Vocalizations

IAN STIRLING, Rapporteur
Canadian Wildlife Service
Department of the Environment
5320 122 Street
Edmonton
Alberta T6H 3S5
Canada

JEAN-PAUL ROUX, Rapporteur[1]
Institut des Sciences de l'Evolution
Section Socio-Ecologie
USTL Place Bataillon
34060 Montpellier Cedex
France

Descriptions to date of vocalizations given in air by the different species of fur seals that are on land during the breeding season are variable in quality and in their subsequent usefulness. In the session, it was agreed that these vocalizations should be described as accurately and quantitatively as possible, as part of the overall description of the behavior of each species. Specific recommendations on methodology included the following:

(1) Good quality tape recordings, with minimal background interference, should be made of each different call in the repertoire of each species. The range of variability within and among individuals should be quantified. It should be recognized ahead of time that this will probably be quite time-consuming.

(2) Recordings should be well documented with either written notes, referenced to the counter on the tape recorder, or with verbal comments recorded onto the tapes. Some important data are:
   — Technical information (weather conditions, type of microphone, distance from the animal, habitat)
   — Emitter's status (age, sex, physiological and reproductive status, social status)
   — Context of the call (spontaneous or in response to a specific event, directed at the observer).

(3) In written descriptions, calls should be illustrated with representative sound spectrograms and a measure of variability. The filters and bandwidths used to make the sound spectrograms should be recorded.

(4) Whenever possible, names assigned to calls should describe their functions (e.g., pup attraction call). If the function is the same as has already been described and named elsewhere, that name should be used rather than another assigned.

(5) When possible, the ascribed function should be verified with playback experiments.

A demonstration tape made for the meeting showed that considerable variability exists in the same call when it is given by different species. Detailed comparisons of species-specific fur seal vocalizations may give some indication of taxonomic relationships within the genus. Particular emphasis should be placed on calls which relate to agonistic, sexual, and maternal behavior. This could be of particular interest when studying *Arctocephalus tropicalis* and *A. gazella* in areas where they appear to be hybridizing or, conversely, in areas where two or more species overlap ranges but do not hybridize. Comparison of the vocalizations of fur seals and sea lions might also be useful in understanding the taxonomic relationships of *A. pusillus* in particular. In some species which have widely separated subpopulations, such as *A. gazella*, *A. tropicalis*, *A. forsteri*, and *A. pusillus*, there may be geographically different dialects such as those described for some species of phocids. If the degree of variability in the vocalizations within one or more species can be documented, it may indicate the value of quantifying differences among species. This is important because in some other species of mammals the calls given by the same population can change through time. Recordings at the same colony over a period of years should indicate whether or not such changes occur in species of *Arctocephalus*.

[1]Present address: Sea-Fisheries, P.O. Box 394, 9000 Lüderitz, S.W.A./Namibia.

Another approach that could give valuable insight into the functions of vocalizations within species is to describe the ontogeny of the calls from pups through adults as well as the annual cycle of the occurrence of different calls. This has not been done for any species of fur seal. Any discussion on agonistic, sexual, or maternal behavior should take studies of the associated vocalizations into account.

Although underwater vocalizations were not discussed at this workshop, there is almost no information on this aspect of fur seal behavior, either during or outside the breeding season. Interpretation is often confounded by the fact that the behavior of the seal giving the calls cannot be observed. Maximum effort should be made to observe and describe the behavior of a seal vocalizing underwater whenever a fortuitous opportunity, or a good location with clear water, presents itself where a hydrophone can be used. Otherwise, the same guidelines apply as are given above for vocalizations given in air.

Fur Seal Diving Behavior

GERALD L. KOOYMAN, Rapporteur
Physiological Research Laboratory
Scripps Institution of Oceanography
University of California, San Diego
La Jolla, California 92093

The discussion of diving studies was centered around four major topics: 1) types of recorders available for monitoring behavior at sea, 2) physiological and behavioral information that can be obtained from recorders now available, 3) gaps in our data base, and 4) physiological limits in various species that set the oceanic boundaries for diving mammals.

The oldest and simplest system used for monitoring behavior at sea uses beacons to emit a simple radio frequency signal; the reception of the signal indicates the presence and sometimes the location of the animal. The most basic use of beacons allows an investigator to determine if a seal or sea lion is ashore, and consequently to determine the duration of the sea period. When used at sea the reception period indicates surface time; if more than one receiver is used, the rate of movement can be determined by triangulation. The last two procedures are very labor-intensive and only one or two such studies have been done.

In the last several years a mechanical time/depth recorder has been employed to record depth against time and surface swimming. From these three variables, other data can be extracted in regard to behavior at sea. The most basic information obtained from the recorders is a time budget for the period at sea. This time budget can be divided into swimming, nonswimming, and diving periods. The diving periods may be further divided into random diving and diving bouts if some kind of dive bout criterion is established, such as a log-survivorship curve analysis of interdive interval.

If the metabolic rate for the various activities is known, then much more detail about the animals' sea activities can be calculated, and many more questions can be asked and hypotheses tested.

Information about energy output and intake is especially critical to any tests of foraging theory which in great part are based on the common currency of energy. This information is also crucial to test the degree to which physiological limitations affect the range and depth of foraging areas. The energy problem has been addressed in two different ways. Doubly-labeled water has been employed to determine the total energy production and consumption over several days. This topic is treated in detail in another discussion section. The other approach has been to measure the animal's metabolic rate while resting and while swimming at known speeds. This kind of analysis is now in progress at two or three different laboratories. Eventually it should be possible to calculate the energy production of a fur seal by determining its specific activities from time/depth and swim speed records, and then matching these activity budgets to known metabolic rates for each activity.

The major problems in making energy estimates are the lack of data on the species of prey consumed and on the swim speeds animals use. The prey species have been assessed from scat samples, but this approach is suitable for only a few species with special behavior patterns. At the present time, diet is a major obstacle to more detailed analysis of foraging energetics. Without swim speeds, it is impossible to calculate the distance animals have traveled to food patches and the cost of the trip. Swim rates are also necessary to calculate the energy expenditure during diving and the breathhold limits. Estimates of swim rates may be available soon from recently developed submersible microprocessors.

Another major gap in information about behavior of fur seals at sea are sex and age differences. Due to the great size difference between females and mature males, both the duration and depth of foraging dives of the males may be longer. If so, where males and females have overlapping foraging areas, the actual feeding depths may not overlap. Immature males may be intermediate between adult females and males in this depth separation. However,

because males do not have to return to shore to feed a pup, they may feed further offshore than do the females. Thus, male/female competition may be avoided by males feeding in deeper water further offshore. Finally, feeding competition may be reduced since males endure long fasts in the summer months when the pups are growing fastest and when the females are being taxed the most to provide adequate milk for the fast growing pups.

In summary, data on the differences between male and female foraging behavior, swim rates, energy consumption, and aerobic limits are required to develop a better understanding of diving patterns of fur seals. To obtain these data for swim rates, new kinds of recording equipment must be developed. Obtaining the data for differences between males and females may only require modifications of available recorders. Energy consumption at sea has been determined by the use of doubly labeled water. When swim rates can be monitored in detail, it may be possible to establish energy budgets by means of time partitioning. Aerobic limits can be calculated but require detailed data on swim rates, metabolic rate, and total available oxygen stores.

APPENDIX 1
List of Contributors

George A. Antonelis, Jr.
NOAA, National Marine Mammal Laboratory
7600 Sand Point Way N.E., Bldg. 4
Seattle, WA 98115 USA

Marthan N. Bester
Mammal Research Institute
University of Pretoria
Pretoria 0002 SOUTH AFRICA

Douglas S. Butterworth
Department of Applied Mathematics
University of Cape Town
Rondebosch 7700 SOUTH AFRICA

John P. Croxall
British Antarctic Survey
Natural Environment Research Council
High Cross, Madingley Road
Cambridge CB30ET UNITED KINGDOM

Jeremy H. M. David
Sea Fisheries Institute
Marine Mammal Laboratory
P.O. Box 251
Capetown 5000 SOUTH AFRICA

Robert L. DeLong
NOAA, National Marine Mammal Laboratory
7600 Sand Point Way N.E., Bldg. 4
Seattle, WA 98115 USA

D. William Doidge
Department of Renewable Resources
MacDonald College of McGill University
21111 Lakeshore Road, Ste-Anne-de-Bellevue
Quebec H9X 1C0 CANADA

Luis A. Fleischer
Centro Regional de Investigacion Pesquera
Km. 1 Carretera a Pichilingue
La Paz, Baja California Sur MEXICO

L. Fletcher
Antarctic Division
Channel Highway, Kingston
Tasmania 7150 AUSTRALIA

Roger L. Gentry
NOAA, National Marine Mammal Laboratory
7600 Sand Point Way N.E., Bldg. 4
Seattle, WA 98115 USA

Carlos Guerra C.
Instituto de Investigaciones Oceanologicas
Universidad de Antofagasta
Camino a Coloso S/N
Casilla 1240
Antofagasta, CHILE

Pierre Jouventin
CEBAS-CNRS
79369 Beauvoir-sur-Niort
FRANCE

Graham I. H. Kerley
Department of Zoology
University of Port Elizabeth
P.O. Box 1600
Port Elizabeth 6001 SOUTH AFRICA

Gerald L. Kooyman
Physiological Research Laboratory
Scripps Institution of Oceanography
University of California, San Diego
La Jolla, CA 92093 USA

John K. Ling
South Australian Museum
North Terrace
Adelaide 5000 AUSTRALIA

Patricia Majluf
Large Animal Research Group
Department of Zoology
University of Cambridge
34A Storey's Way
Cambridge CB3 ODT UNITED KINGDOM

Robert H. Mattlin
Fisheries Research Division
P.O. Box 297
Wellington NEW ZEALAND

T. Seamus McCann
British Antarctic Survey
Natural Environment Research Council
High Cross, Madingley Road
Cambridge CB3 OET UNITED KINGDOM

Lesley H. (Rickett) McQuaid
Department of Zoology
Rhodes University
P.O. Box 94
Grahamstown 6140 SOUTH AFRICA

Mark O. Pierson
Institute for Marine Studies
University of California
Santa Cruz, CA 95064 USA

Alberto Ponce de Leon
Departamento de Oceanografia
Facultad de Humanidades y Ciencias
Tristan Narvaja 1674
Montevideo, URUGUAY

Terrence J. Robinson
Mammal Research Institute
University of Pretoria
Pretoria 0002 SOUTH AFRICA

Jean-Paul Roux
Sea-Fisheries
P.O. Box 394
9000 Lüderitz, S.W.A./NAMIBIA

Peter D. Shaughnessy
CSIRO Institute of Biological Resources
Box 225 Dickson
ACT 2602 AUSTRALIA

Brent S. Stewart
Hubbs Marine Research Center
1700 South Shores Rd.
San Diego, CA 92109 USA

Ian Stirling
Canadian Wildlife Service
Department of the Environment
5320 122 Street
Edmonton, Alberta T6H 3S5 CANADA

Daniel Torres N.
Subdireccion Cientifica
Instituto Antártico Chileno
Luis Thayer Ojeda 814, Correo 9
Santiago, CHILE

Fritz Trillmich
Max-Planck-Institut für Verhaltensphysiologie
Abteilung Wickler
D-8131 Seewiesen, W. GERMANY

Raul Vaz-Ferreira
Departamento de Zoologia de Vertebrados
Facultad de Humanidades y Ciencias
Tristan Narvaja 1674
Montevideo, URUGUAY

Valery A. Vladimirov
VNIRO
17 F. Krasnoselskaya
Moscow B-140 USSR

Robert M. Warneke
Arthur Rylah Institute for Environmental Research
Box 137 Heidelberg
Victoria 3084, AUSTRALIA

Sibusiso S. Xulu
Department of Applied Mathematics
University of Zululand
Private Bag X1001
Kwa-dlangezwa 3886 SOUTH AFRICA

Pamela K. Yochem
Hubbs Marine Research Center
1700 South Shores Rd.
San Diego, CA 92109 USA

Anne E. York
NOAA, National Marine Mammal Laboratory
7600 Sand Point Way N.E., Bldg. 4
Seattle, WA 98115 USA

APPENDIX 2
Fur Seal Bibliography 1976-86

CHRISTINE M. PHILLIPS, compiler
British Antarctic Survey
National Environment Research Council
High Cross, Madingley Road,
Cambridge CB3 OET, United Kingdom

INTRODUCTION

This bibliography was originally compiled for circulation to participants at the international fur seal symposium held at the British Antarctic Survey, Cambridge, in April 1984. Since it was intended as a working bibliography, it included only publications since 1976 which were part of the British Antarctic Survey (BAS) collection. The bibliography which follows has been expanded to include all known publications from 1976 to September 1986, beyond those contained in the BAS collection. The main sources used to trace relevant papers were: BAS library catalogues; Ronald et al. 1983; Aquatic Sciences and Fisheries Abstracts; Antarctic Bibliography; and Current Antarctic Literature. The bibliography has been made as comprehensive as possible, but inevitably some papers will have been missed. The only category deliberately excluded is published abstracts.

ABBOTT, I.
1979. The past and present distribution and status of sea lions and fur seals in Western Australia. Rec. West. Aust. Mus. 7:375-390.

AGUAYO, A.
1978. The present status of the Antarctic fur seal *Arctocephalus gazella* at South Shetland Islands. Polar Rec. 19:167-176.
1979. Juan Fernandez fur seal. *In* Mammals in the seas, p. 28-30. FAO Fish. Ser. 5, Vol. II.

AGUAYO, A., R. MATURANA, and D. TORRES.
1977. El lobo fino antartico, *Arctocephalus gazella* (Peters), en el Sector Antartico Chileno (Pinnipedia - Otariidae). Ser. Cient. Inst. Antart. Chileno 5:5-16.

ARNOLD, W., and R. TRILLMICH.
1985. Time budget in Galapagos fur seal pups: the influence of the mother's presence and absence on pup activity and play. Behaviour 92:302-321.

BABA, N., K. YOSHIDA, and T. TCHIHARA.
1979. An application of radio wave telemetry to the study of fur seals' (*Callorhinus ursinus*) behavior on the breeding islands. Bull. Far Seas Fish. Res. Lab. 17:177-195.

BAKER, J. R., and D. W. DOIDGE.
1984. The pathology of the Antarctic fur seal (*Arctocephalus gazella*) in South Georgia. Br. Vet. J. 140:210-220.

BATALLES, L. M., M. LIMA, A. MALEK, and A. PONCE de LEON.
1985. Estudio sobre porcentajes de prenez en el lobo sudamericano *Arctocephalus australis* (Zimmermann, 1783) para 1985 en Uruguay. Contrib. Cient. Industria Lobera y Pesquera del Estado 1(2):11-20.

BEST, P. B., M. A. MEYER, and R. W. WEEKS.
1981. Interactions between a male elephant seal *Mirounga leonina* and Cape fur seals *Arctocephalus pusillus*. S. Afr. J. Zool. 16:59-66.

BESTER, M. N.
1977. Habitat selection, seasonal population changes, and behaviour of the Amsterdam fur seal, *Arctocephalus tropicalis*, on Gough Island. D.Sc. thesis, Univ. Pretoria, 193 p.
1980. Population increase in the Amsterdam Island fur seal *Arctocephalus tropicalis* at Gough Island. S. Afr. J. Zool. 15:229-234.
1981. Fur seals *Arctocephalus gazella* and leopard seals *Hydrurga leptonyx* at the Courbet Peninsula, Kerguelen. S. Afr. J. Antarct. Res. 10/11:35-37.
1981. Seasonal changes in the population composition of the fur seal *Arctocephalus tropicalis* at Gough Island. S. Afr. J. Wildl. Res. 11:49-55.
1982. Distribution, habitat selection and colony types of the Amsterdam Island fur seal *Arctocephalus tropicalis* at Gough Island. J. Zool. 196:217-231.
1984. Status of the population of the fur seals *Arctocephalus tropicalis* and *Arctocephalus gazella* north of the Antarctic Convergence. S. Afr. J. Sci. 80:27-28.

BESTER, M. N., and G. I. H. KERLEY.
1983. Rearing of twin pups to weaning by subantarctic fur seal *Arctocephalus tropicalis* female. S. Afr. J. Wildl. Res. 13:86-87.

BESTER, M. N., and P. A. LAYCOCK.
1985. Cephalopod prey of the sub-Antarctic fur seal, *Arctocephalus tropicalis*, at Gough Island. *In* Siegfried, W. R., P. R. Condy, and R. M. Laws (eds.), Antarctic nutrient cycles and food webs, p. 551-554. Springer-Verlag, Berlin.

BIGG, M. A.
1984. Stimuli for parturition in northern fur seals (*Callorhinus ursinus*). J. Mammal. 65:333-336.

BIGG, M. A., and I. FAWCETT.
1985. Two biases in diet determination of northern fur seals (*Callorhinus ursinus*). *In* Beddington, J. R., R. J. H. Beverton, and D. M. Lavigne (eds.), Marine mammals and fisheries, p. 284-291. George Allen and Unwin, London.

BIGG, M. A., I. B. MacASKIE, and G. ELLIS.
1978. Studies on captive fur seals. Manuscr. Rep., Fish. Res. Board Can., No. 1471, 21 p.

BLIX, A. S., L. K. MILLER, M. C. KEYES, H. J. GRAV, and R. ELSNER.
1979. Newborn northern fur seals (*Callorhinus ursinus*) - do they suffer from cold? Am. J. Physiol. 236:R322-R327.

BOGDANOV, L. V., V. A. CHERNOLVANOV, and V. I. PLYAKOVSKII.
1977. Biochemical polymorphism of the northern fur seal, *Callorhinus ursinus*, from three regions of the Northwest Pacific. Genetics 13:1008-1014.

BONNER, W. N.
1979. Antarctic (Kerguelen) fur seal. *In* Mammals in the seas, p. 49-51. FAO Fish. Ser. 5, Vol. II.
1979. Subantarctic fur seal. *In* Mammals in the seas, p. 52-54. FAO Fish. Ser. 5, Vol. II.
1981. Southern fur seals *Arctocephalus* (Geoffroy Saint-Hilaire and Cuvier, 1826). *In* Ridgway, S. H., and R. J. Harrison (eds.), Handbook of marine mammals, Vol. 1, p. 143-160. Acad. Press, London.
1982. The status of the Antarctic fur seal *Arctocephalus gazella*. *In* Mammals in the seas, p. 423-430. FAO Fish. Ser. 5, Vol. IV.
1984. Lactation strategies in pinnipeds: problems for a marine mammalian group. *In* Peaker, M., R. G. Vernon, and C. H. Knight (eds), Physiological strategies in lactation. Symp. Zool. Soc. Lond. 51:253-272.
1984. Seals of the Galapagos Islands. Biol. J. Linn. Soc. 21:177-184.
1985. Antarctic fur seals. Biologist 32:177-182.
1985. Impact of fur seals on the terrestrial environment at South Georgia. *In* Siegfried, W. R., P. R. Condy, and R. M. Laws (eds.), Antarctic nutrient cycles and food webs, p. 641-646. Springer-Verlag, Berlin.

BONNER, W. N., and S. HUNTER.
1982. Predatory interactions between Antarctic fur seals, macaroni penguins and giant petrels. Br. Antarct. Surv. Bull. 56:75-79.

BONNER, W. N., and T. S. McCANN.
1982. Neck collars on fur seals, *Arctocephalus gazella*, at South Georgia. Br. Antarct. Surv. Bull. 57:73-77.
BRYDEN, M. M., and G. S. MOLYNEUX.
1978. Arteriovenous anastomoses in the skin of seals. Part 2. The California sea lion, *Zalophus californianus*, and the northern fur seal, *Callorhinus ursinus*, Pinnipedia, Otariidae. Ant. Rec. 191:253-260.
CALAMBOKIDIS, J., and R. L. GENTRY.
In press. Mortality of known history northern fur seal pups. J. Wildl. Dis.
CARDENAS, J. C., and J. YANEZ.
1983. Variaciones extremas de color del lobo fino antartico *Arctocephalus gazella* (Peters, 1875) en Islas Shetland del Sur, Chile. Ser. Cient. Inst. Antart. Chileno 30:5-12.
CARNIO, J.
1982. Observations on the mother and young interactions in captive Cape fur seals. Aquat. Mamm. 9(2):50-56.
CARR, T., N. CARR, and J. H. M. DAVID.
1985. A record of the sub-Antarctic fur seal *Arctocephalus tropicalis* in Angola. S. Afr. J. Zool. 20:77.
CASTELLO, H. P., and M. C. PINEDO.
1977. *Arctocephalus tropicalis*, first record for Rio Grande do Sul coast (Pinnipedia, Otariidae). Atl. Rio Grande 2:111-119.
CATTAN, P. E., J. YANEZ, D. TORRES, M. GAJARDO, and J. C. CARDENAS.
1982. Censo, marcaje y estructura poblacional del lobo fino antartico *Arctocephalus gazella* (Peters, 1875) en las islas Shetland del Sur, Chile. Ser. Cient. Inst. Antart. Chileno 29:31-38.
CAVAGNOLO, R. Z., and N. A. VEDROS.
1978. Identification and characterization of three immunoglobulin classes in the northern fur seal *Callorhinus ursinus*. Dev. Comp. Immunol. 2:689-697.
1979. Serum and colostrum immunoglobulin levels in the northern fur seal, *Callorhinus ursinus*. Dev. Comp. Immunol. 3:139-146.
CAWTHORN, M. W., M. C. CRAWLEY, R. H. MATTLIN, and G. J. WILSON.
1985. Research on pinnipeds in New Zealand. A report prepared by the Pinniped Research Review Sub-committee. Wildl. Res. Liaison Group Res. Rev. No. 7, 29 p.
CHAPMAN, D. G.
1981. The northern fur seal - an example of complexity. *In* Jewell, P. A., and S. Holt (eds.), Problems in management of locally abundant wild mammals, p. 193-204. Acad. Press, New York.
CHELNOKOV, F. G.
1977. [Yield prediction of bachelor fur seals and dynamics of bull numbers on the southeastern rookery of Medny I.] Morskie Mlekopitaiushchie Tikhogo Okeana 1:18-34. (In Russian.)
1978. [On mortality of fur seal pups (*Callorhinus ursinus*) (Mammalia: Otariidae) on Medny Island rookery in connection with their counting and tagging.] Vestn. Zool. 12:85-87. (In Russian.)
1981. [Dynamics of the age composition of fur seal females on the hauling-out grounds of Medny Islands in 1970-1977.] Izv. TINRO 105:146-151. (In Russian.)
1982. [On the mixing of fur seals from the Commodore Islands with other populations.] Vopr. Geogr. Kamchatki 8:74-76. (In Russian.)
1984. Abundance of sea lions and their relationship with fur seals at the southeastern hauling ground of Mednyi Island (Commander Islands). Sov. J. Mar. Biol. 9:193-195.
CHUGUNKOV, D. I.
1982. [On the abundance of fur seals and northern sea-lions from the northwestern hauling-out ground on Bering I. in autumn and winter.] Vopr. Geogr. Kamchtki 8:72-74. (In Russian.)
CHUPAKHINA, T. I.
1977. [Mass increase in suckling fur seal pups.] Morskie Mlekopitaiushchie Tikhogo Okeana 1:46-49. (In Russian.)
CLARK, T. W.
1979. Galapagos fur seal. *In* Mammals in the seas, p. 31-33. FAO Fish. Ser. 5, Vol. II.
CLARKE, M. R., and F. TRILLMICH.
1980. Cephalopods in the diet of fur seals of the Galapagos Islands. J. Zool. 190:211-215.
CONDY, P. R.
1978. Distribution, abundance, and annual cycle of fur seals (*Arctocephalus* spp.) on the Prince Edward Islands. S. Afr. J. Wildl. Res. 8:159-168.
1981. Annual food consumption, and seasonal fluctuations in biomass of seals at Marion Island. Mammalia 45:21-30.
CONDY, P. R., and E. D. GREEN.
1980. The fur coat of the Amsterdam Island fur seal, *Arctocephalus tropicalis*. J. Zool. 191:85-96.
COSTA, D. P., and R. L. GENTRY.
1986. Free-ranging energetics of northern fur seals. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur seals. Maternal strategies on land and at sea, p. 79-101. Princeton Univ. Press, Princeton.
CRAWLEY, M. C., J. D. STARK, and P. S. DODGSHUN.
1977. Activity budgets of New Zealand fur seals, *Arctocephalus forsteri*, during the breeding season. N.Z. J. Mar. Freshw. Res. 11:777-788.
CRAWLEY, M. C., and R. WARNEKE.
1979. New Zealand fur seal. *In* Mammals in the seas, p. 45-48. FAO Fish. Ser. 5, Vol. II.
CRAWLEY, M. C., and G. J. WILSON.
1976. The natural history and behaviour of the New Zealand fur seal (*Arctocephalus forsteri*). Tuatara 22:1-29.
CROXALL, J. P., I. EVERSON, G. L. KOOYMAN, C. RICKETTS, and R. W. DAVIS.
1985. Fur seal diving behaviour in relation to vertical distribution of krill. J. Anim. Ecol. 54:1-8.
CROXALL, J. P., and M. N. PILCHER.
1984. Characteristics of krill *Euphausia superba* eaten by Antarctic fur seals *Arctocephalus gazella* at South Georgia. Br. Antarct. Surv. Bull. 63:117-125.
DAVID, J. H. M., and R. W. RAND.
1986. Attendance behavior of South African fur seals. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur seals. Maternal strategies on land and at sea, p. 126-141. Princeton Univ. Press, Princeton.
De GRAAF, A. S., P. D. SHAUGHNESSY, R. M. McCULLY, and A. VERSTER.
1980. Occurrence of *Taenia solium* in a Cape fur seal *Arctocephalus pusillus*. Onderstepoort J. Vet. Res. 47:119-120.
DEVILLIERS, A. F., and G. J. B. ROSS.
1976. Notes on numbers and distribution of fur seals, *Arctocephalus tropicalis* (Gray), on Marion and Prince Edward Islands, Southern Ocean. J. Mammal. 57:595-600.
DIERAUF, L. A.
1984. A northern fur seal, *Callorhinus ursinus*, found in the Sacramento-San Joaquin Delta. Calif. Fish Game 70(3):189.
DOBRORUKA, L. J.
1976. Play behaviour in the South African fur seal, *Arctocephalus pusillus*. Lynx (Prague) 18:131.
DOIDGE, D. W., and J. P. CROXALL.
1985. Diet and energy budget of the Antarctic fur seal, *Arctocephalus gazella*, at South Georgia. *In* Siegfried, W. R., P. R. Condy, and R. M. Laws (eds.), Antarctic nutrient cycles and food webs, p. 543-550. Springer-Verlag, Berlin.
DOIDGE, D. W., J. P. CROXALL, and J. R. BAKER.
1984. Density-dependent pup mortality in the Antarctic fur seal *Arctocephalus gazella* at South Georgia. J. Zool. 202:449-460.
DOIDGE, D. W., J. P. CROXALL, and C. RICKETTS.
1984. Growth rates of Antarctic fur seal *Arctocephalus gazella* pups at South Georgia. J. Zool. 203:87-93.
DOIDGE, D. W., T. S. McCANN, and J. P. CROXALL.
1986. Attendance behavior of Antarctic fur seals. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur seals. Maternal strategies on land and at sea, p. 102-114. Princeton Univ. Press, Princeton.
DOSAKO, S., S. TANEYA, T. KIMURA, T. OHMORI, H. DAIKOKU, N. SUZUKI, J. SAWA, K. MANO, and S. KATAYAMA.
1983. Milk of northern fur seal: composition, especially carbohydrate and protein. J. Dairy Sci. 66:2076-2083.
EBERHARDT, L. L.
1981. Population dynamics of the Pribilof fur seals. *In* Fowler, C. W., and T. D. Smith (eds.), Dynamics of large mammal populations, p. 197-220. Wiley, New York.
ENGEL, R. M., R. H. LANDER, A. Y. ROPPEL, P. KOZLOFF, J. R. HARTLEY, and M. C. KEYES.
1980. Population data, collection procedures, and management of the northern fur seal, *Callorhinus ursinus*, of the Pribilof Islands, Alaska. Prog. Rep. 80-11, Natl. Mar. Fish. Serv., NOAA, Northw. Alaska Fish. Cent., Seattle, WA, 212 p.
ENGLISH, A. W.
1976. Functional anatomy of the hands of fur seals and sea lions. Am. J. Anat. 147:1-17.
1977. Structural correlates of fore limbs function in fur seals and sea lions. J. Morphol. 151:325-353.
FISCUS, C. H.
1978. Northern fur seal. *In* Haley, D. (ed.), Marine mammals of eastern North Pacific and Arctic Waters, p. 153-159. Pacific Search Press, Seattle, WA.

FLEISCHER, L. A.
1978. The distribution, abundance, and population characteristics of the Guadalupe fur seal, *Arctocephalus townsendi* (Merriam 1897). M.Sc. thesis, Univ. Wash., Seattle, 93 p.
1978. Guadalupe fur seal. *In* Haley, D. (ed.), Marine mammals of eastern North Pacific and Arctic waters, p. 161-165. Pacific Search Press, Seattle, WA.
FLETEMEYER, J. R.
1978. Laminae in the teeth of the Cape fur seal used for age determination. Life Sci. 22:695-698.
FOWLER, C. W.
1982. Interactions of northern fur seals and commercial fisheries. Trans. 47th N. Am. Wildl. Nat. Resour. Conf., p. 278-292.
FOWLER, C. W., and T. R. MERRELL.
1986. Victims of plastic technology. Alaska Fish and Game 18(2):34-37.
FRISMAN, E. Ya., E. I. SKALETSKAYA, and A. E. KUZIN.
1982. A mathematical model of the population dynamics of a local northern fur seal herd. Ecol. Model. 16:151-172.
FUENTES TAPIA, H., and H. TOVAR SERPA.
1978. [The population of fur seals in December of 1978.] Informe, Inst. del Mar del Peru 66, 17 p. (In Spanish.)
GALANTSEV, V. P., and M. K. MAMINOV.
1979. [Differences in the function of cardiac automatism between the pups of Kuril seal (*Phoca vitulina kurilensis*) and fur seal (*Callorhinus ursinus*).] Zool. Zh. 58:1565-1573. (In Russian.)
GENTRY, R. L.
1980. Set in their ways: survival formula of the northern fur seal. Oceans 13(3):34-37.
1981. Land-sea movements of northern fur seals relative to commercial harvesting. *In* Chapman, J. A., and D. Pursley (eds.), Proc. Worldwide Furbearer Conference, Frostburg, MD, Aug. 3-11, 1980, Vol. 2, p. 1328-1359. Worldwide Furbearer Conference, Inc., Frostburg, MD.
1981. Northern fur seal *Callorhinus ursinus* (Linnaeus, 1758). *In* Ridgway, S. H., and R. J. Harrison (eds.), Handbook of marine mammals, Vol. 1, p. 143-160. Acad. Press, Lond.
1981. Seawater drinking in eared seals. Comp. Biochem. Physiol. 68A:81-86.
GENTRY, R. L., D. P. COSTA, J. P. CROXALL, J. H. M. DAVID, R. W. DAVIS, G. L. KOOYMAN, P. MAJLUF, T. S. McCANN, and F. TRILLMICH.
1986. Synthesis and conclusions. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur seals. Maternal strategies on land and at sea, p. 220-264. Princeton Univ. Press, Princeton.
GENTRY, R. L., and J. R. HOLT.
1982. Equipment and techniques for handling northern fur seals. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF 758, 15 p.
1986. Attendance behavior of northern fur seals. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur seals. Maternal strategies on land and at sea, p. 41-60. Princeton Univ. Press, Princeton.
GENTRY, R. L., and J. H. JOHNSON.
1981. Predation by sea lions on northern fur seal neonates. Mammalia 45:423-430.
GENTRY, R. L., and G. L. KOOYMAN (editors).
1986. Fur seals. Maternal strategies on land and at sea. Princeton Univ. Press, Princeton, NJ, 291 p.
1986. Introduction. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur seals. Maternal strategies on land and at sea, p. 3-27. Princeton Univ. Press, Princeton.
1986. Methods of dive analysis. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur seals. Maternal strategies on land and at sea, p. 28-40. Princeton Univ. Press, Princeton.
GENTRY, R. L., G. L. KOOYMAN, and M. E. GOEBEL.
1986. Feeding and diving behavior of northern fur seals. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur seals. Maternal strategies on land and at sea, p. 61-78. Princeton Univ. Press, Princeton.
GRAV, H. J., and A. S. BLIX.
1979. A source of nonshivering thermogenesis in fur seal skeletal muscle. Science 204:87-89.
GRIBEN, M. R.
1979. A study of the intermixture of subadult male fur seals *Callorhinus ursinus* (Linnaeus 1758) between the Pribilof Islands of St. George and St. Paul, Alaska. M.Sc. thesis, Univ. Wash., Seattle, 191 p.
GRIBEN, M. R., H. R. JOHNSON, B. B. GALLUCCI, and V. F. GALLUCCI.
1984. A new method to mark pinnipeds as applied to the northern fur seal. J. Wildl. Manage. 48:945-949.
HADLOW, W. J., N. F. CHEVILLE, and W. L. JELLISON.
1980. Occurrence of pox in a northern fur seal on the Pribilof Islands in 1951. J. Wildl. Dis. 16:305-312.
HUBBS, C. L.
1979. Guadalupe fur seal. *In* Mammals in the seas, p. 24-27. FAO Fish. Ser. 5, Vol. II.
HUNTER, L., and S. H. MADIN.
1976. Clinical blood values of the northern fur seal, *Callorhinus ursinus*. J. Wildl. Dis. 12:526-530.
1978. Clinical blood values of the northern fur seal, *Callorhinus ursinus*. II. Comparison of fresh versus stored frozen serum. J. Wildl. Dis. 14:116-119.
1978. Clinical blood values of the northern fur seal, *Callorhinus ursinus*. III. Comparison of eye fluid and serum values. J. Wildl. Dis. 14:176-177.
JOUVENTIN, P., J. C. STAHL, and H. WEIMERSKIRCH.
1982. La recolonisation des Iles Crozet par les otaries (*Arctocephalus tropicalis* et *A. gazella*). Mammalia 46:505-514.
KAJIMURA, H.
1984. Opportunistic feeding of the northern fur seal, *Callorhinus ursinus*, in the eastern North Pacific Ocean and eastern Bering Sea. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF 779, 49 p.
1985. Opportunistic feeding by the northern fur seal, (*Callorhinus ursinus*). *In* Beddington, J. R., R. J. H. Beverton, and D. M. Lavigne (eds.), Marine mammals and fisheries, p. 300-318. George Allen and Unwin, London.
KAJIMURA, H., C. H. FISCUS, and R. K. STROUD.
1981. Food of the Pacific white sided dolphin, *Lagenorhynchus obliquidens*, Dalls porpoise, *Phocoenoides dalli*, and northern fur seal, *Callorhinus ursinus*, off California and Washington. NOAA Tech. Memo. NMFS F/NWC 2, Northwest Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA, 30 p.
KERLEY, G. I. H.
1983. Comparison of seasonal haul-out patterns of fur seals *Arctocephalus tropicalis* and *A. gazella* on subantarctic Marion Island. S. Afr. J. Wildl. Res. 13:71-77.
1983. Record for the Cape fur seal *Arctocephalus pusillus pusillus* from subantarctic Marion Island. S. Afr. J. Zool. 18:139-140.
1984. Relationships between sympatric breeding populations of fur seals (*Arctocephalus* spp.) at the Prince Edward Islands. S. Afr. J. Sci. 80:28-29.
1985. Pup growth in the fur seals *Arctocephalus tropicalis* and *A. gazella* on Marion Island. J. Zool. Ser. A, 205:315-324.
KERLEY, G. I. H., and M. N. BESTER.
1983. A note on whole-mass corrections from piecemeal determinations for fur seals. S. Afr. J. Wildl. Res. 13:49-50.
KIGHTLEY, S. P. J., and J. R. CALDWELL.
1982. The first record of a fur seal birth on Signy Island, South Orkney Islands. Br. Antarct. Surv. Bull. 51:287-289.
KING, J. E.
1976. On the identity of three young fur seals (genus *Arctocephalus*) stranded in New Caledonia (Mammalia, Pinnipedia). Beaufortia 25(324):97-105.
KOLESNIK, I. A., and A. A. TIMOFEEVA.
1980. [Some features of growth, nutrition, and production of fur seal, *Callorhinus ursinus*, pups of Tyuleny Island, Russian SFSR, USSR.] Izv. Akad. Nauk SSSR Ser. Biol. 3:433-441. (In Russian.)
KOLESNIK, I. A., A. A. TIMOFEEVA, and T. I. CHUPAKHINA.
1977. [An estimate of the population density of fur seals (*Callorhinus ursinus*) on Tyuleni Island).] Zool. Zh. 56:1085-1091. (In Russian.)
KOLESNIK, I. A., A. A. TIMOFEEVA, V. G. POMIKALOV, and T. I. CHUPAKHINA.
1978. [Correlation and spectral analysis of population abundance of the fur seal on Tyuleni Island (Sea of Okhotsk).] Zool. Zh. 57:115-123. (In Russian.)
KOOYMAN, G. L.
1982. Development and testing of a time-depth recorder for marine mammals. U.S. Mar. Mamm. Comm. Rep. MMC-76/23, 10 p.
KOOYMAN, G. L., J. O. BILLUPS, R. W. DAVIS, and M. A. CASTELLINI.
1977. Diving behavior of fur seals, *Arctocephalus gazella*, and King penguins, *Apenodytes patagonica*, near South Georgia island. Antarct. J. U.S. 12(4):8.
KOOYMAN, G. L., and R. W. DAVIS.
1980. Feeding behavior of female Antarctic fur seals, *Arctocephalus gazella*. Antarct. J. U.S. 15(5):159-160.
KOOYMAN, G. L., R. W. DAVIS, and J. P. CROXALL.
1986. Diving behavior or Antarctic fur seals. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur seals. Maternal strategies on land and at sea, p. 115-125. Princeton Univ. Press, Princeton.
KOOYMAN, G. L., and R. L. GENTRY.
1986. Diving behavior of South African fur seals. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur seals. Maternal strategies on land and at sea, p. 142-152. Princeton Univ. Press, Princeton.
KOOYMAN, G. L., R. L. GENTRY, and D. L. URQUHART.
1976. Northern fur seal diving behavior: a new approach to its study. Science 193:411-412.

KOOYMAN, G. L., and F. TRILLMICH.
1986. Diving behavior of Galapagos fur seals. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur seals. Maternal strategies on land and at sea, p. 186-195. Princeton Univ. Press, Princeton.
KOZLOFF, P. (editor).
1980. Fur seal investigations, 1979. NWAFC Proc. Rep. 80-4, Northwest Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115, 93 p.
1981. Fur seal investigations, 1980, NWAFC Proc. Rep. 81-2, Northwest Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115, 96 p.
1985. Fur seal investigations, 1983. NOAA Tech. Memo. NMFS F/NWC 78, Northwest Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115, 77 p.
KURTZ, D. A., and K. C. KIM.
1976. Chlorinated hydrocarbon and polychlorinated biphenyl residues in tissues and lice of northern fur seals, 1972. Pestic. Monit. J. 10:79-83.
KUZIN, A. E., and G. K. PANINA.
1977. [Age-sex structure and reproductive capacity of the Robben I. fur seal population.] *In* Issledovaniya po biologii ryb i promyslovoi okeanografii 8:98-105. TINRO, Vladivostok. (In Russian.)
1977. [Migrations and distribution of female fur seals in the Northwest Pacific in relation to their physiological state.] Morskie Mlekopitaiushchie Tikhogo Okeana 1:3-17. (In Russian.)
KUZIN, A. E., G. K. PANINA, and A. S. PERLOV.
1977. [Relations between northern fur seals and sea lions on common harem rookeries of the Kuril Is.] Morskie Mlekopitaiushchie Tikhogo Okeana 1:50-66. (In Russian.)
KUZIN, A. E., E. I. SKALETSKAYA, and E. Ya. FRISMAN.
1978. [Estimation of the optimum exploitation rate of the northern fur seal population.] *In* Issledovaniya po biologii ryb i promyslovoi okeanografii 9:153-160. TINRO, Vladivostok. (In Russian.)
LADYGINA, T. F., V. V. POPOV, and A. Ya. SUPIN.
1985. [Somatotopic projections to cerebral cortex of fur seal.] Neurofiziologiya 17:344-351. (In Russian.)
LANDER, R. H.
1979. Alaskan or Northern fur seal. *In* Mammals in the seas, p. 19-23. FAO Fish. Ser. 5, Vol. II.
1979. Role of land and ocean mortality in yield of male Alaskan fur seal, *Callorhinus ursinus*. Fish. Bull. U.S. 77:311-314.
1981. A life table and biomass estimate for Alaskan fur seals. Fish. Res. 1:55-70.
LANDER, R. H. (editor).
1980. Summary of northern fur seal data and collection procedures. Vol. 1: Land data of the United States and Soviet Union (excluding tag and recovery records). NOAA Tech. Memo. NMFS F/NWC 3, Northwest Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115, 315 p.
1980. Summary of northern fur seal data and collection procedures. Vol. 2: Eastern Pacific pelagic data of the United States and Canada (excluding fur seals sighted). NOAA Tech. Memo. NMFS F/NWC 4, Northwest Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115, 541 p.
LANDER, R. H., and H. KAJIMURA (editors).
1980. Summary of northern fur seal data and collection procedures. Vol. 3: Western Pacific pelagic data of the Soviet Union and Japan, 1958-1978 (excluding fur seals sighted). NOAA Tech. Memo. NMFS F/NWC 5, Northwest Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115, 304 p.
1982. Status of northern fur seals. *In* Mammals in the seas, p. 319-345. FAO Fish. Ser. 5, Vol. IV.
LAWS, R. M.
1984. Seals. *In* Laws, R. M. (ed.), Antarctic ecology, Vol. 2, p. 621-715. Academic Press, London.
LIMA, M., and L. M. BATALLES.
1985. Analisis estadistico sobre las relaciones craneales en el lobo sudamericano *Arctocephalus australis* (Zimmermann, 1783). Contrib. Cient. Industria Lobera y Pesquera del Estado 1(1):1-10.
LIMBERGER, D., F. TRILLMICH, G. L. KOOYMAN, and P. MAJLUF.
1983. Reproductive failure of fur seals in Galapagos and Peru in 1982-83. Trop. Ocean Atmos. Newsl. 21:16-17.
LLOYD, D. S., C. P. McROY, and R. H. DAY.
1981. Discovery of northern fur seals (*Callorhinus ursinus*) breeding on Bogoslof Island, southeastern Bering Sea. Arctic 34:318-320.
LYONS, E. T., and M. C. KEYES.
1978. Observations on the infectivity of parasitic third-stage larvae of *Lucasi*, Stiles 1901 (Nematoda: Ancylostomatidae) of northern fur seal, *Callorhinus ursinus*, L., on St. Paul Island, Alaska. J. Parasitol. 64:6454-6458.
1984. Further indication of viability of larvae of the hookworm (*Ucinaria lucasi*) for several years in tissues of northern fur seals (*Callorhinus ursinus*). J. Parasitol. 70:459-460.
LYONS, E. T., M. C. KEYES, and J. CONLOGUE.
1978. Activities of dichlorvos or disophenol against the hookworm (*Ucinaria lucasi*) and sucking lice of northern fur seal (*Callorhinus ursinus*) on St. Paul Island, Alaska. J. Wildl. Dis. 14:455-464.
LYONS, E. T., K. C. KIM, and M. C. KEYES.
1980. Variable activity of disophenol against hookworms and lice of northern fur seal pups on St. Paul Island, Alaska. J. Wildl. Dis. 16:53-58.
McCANN, T. S.
1980. Territoriality and breeding behaviour of adult male Antarctic fur seal, *Arctocephalus gazella*. J. Zool. 192:295-310.
McNAB, A. G., and M. C. CRAWLEY.
1975. Mother and pup behaviour of the New Zealand fur seal, *Arctocephalus forsteri* (Lesson). Mauri Ora 3:77-88.
MACY, S. K.
1982. Mother-pup interactions in the northern fur seal. Ph.D. thesis, Univ. Wash., Seattle.
MAJLUF, P., and F. TRILLMICH.
1981. Distribution and abundance of sea lions (*Otaria byronia*) and fur seals (*Arctocephalus australis*) in Peru. Z. Saugetierkd. 46:384-393.
MAKITA, M., K. YOSHIDA, and N. BABA.
1979. A radio wave telemetry system for the study of fur seals' behavior on the breeding islands. Bull. Far Seas Fish. Res. Lab. 17:197-222.
MATTLIN, R. H.
1978. Population biology, thermoregulation and site preference of the New Zealand fur seal, *Arctocephalus forsteri* (Lesson, 1828), on the Open Bay Islands, New Zealand. Ph.D. thesis, Univ. Canterbury, New Zealand, 179 p.
1978. Pup mortality of the New Zealand fur seal (*Arctocephalus forsteri* Lesson). N.Z. J. Ecol. 1:138-144.
1981. Pup growth of the New Zealand fur seal *Arctocephalus forsteri* on the Open Bay Islands, New Zealand. J. Zool. 193:305-314.
MILLER, L. K.
1978. Energetics of the northern fur seals in relation to climate and food resources of the Bering Sea. U.S. Mar. Mamm. Comm. Rep. MMC-75/08, 27 p.
MOYES, A. B., and D. W. DOIDGE.
1984. Composition of the mineral phase of dentine in southern elephant seal and Antarctic fur seal teeth. Br. Antarct. Surv. Bull. 64:81-84.
MUZHCHINKIN, V. F.
1976. [On some growth patterns of fur seals (*Callorhinus ursinus*).] Zool. Zh. 60: 275-276. (In Russian.)
NIE, C. J. van.
1983. A comparative study of the morphology and the topography of the heart of the *Arctocephalus australis* (fur or ursine seal) and of the heart of the *Phoca vitulina vitulina* (common or harbour seal) in their relation to the type of locomotion. Aquat. Mamm. 10(3):79-82.
NORTH, A. W., J. P. CROXALL, and D. W. DOIDGE.
1983. Fish prey of the Antarctic fur seal *Arctocephalus gazella* at South Georgia. Br. Antarct. Surv. Bull. 61:27-37.
NORTH PACIFIC FUR SEAL COMMISSION.
1980. Report on investigations during 1973-76. N. Pac. Fur Seal Comm., Wash., D.C., 197 p.
1984. Report on investigations during 1977-80. N. Pac. Fur Seal Comm., Wash., D.C., 198 p.
OBENDORF, D. L., and P. J. A. PRESIDENTE.
1978. Foreign body perforation of the esophagus initiating traumatic pericarditis in an Australian fur seal. J. Wildl. Dis. 14:451-454.
OHATA, C. A., and L. K. MILLER.
1977. Some temperature responses of northern fur seal (*Callorhinus ursinus*) pups. J. Mammal. 58:438-440.
OHATA, C. A., L. K. MILLER, and H. KAJIMURA.
1977. Northern fur seal thermoregulation: thermal responses to pelagic conditions. J. Therm. Biol. 2:141-143.
OKYMOTO, H.
1980. Related groups of northern fur seal in the northern part of the Pacific Ocean and their mixing. Heredity (Tokyo) 34:58-65.
PAYNE, M. R.
1977. Growth of a fur seal population. Philos. Trans. R. Soc. Lond., Ser. B, Biol. Sci. 279:67-79.
1978. Population size and age determination in the Antarctic fur seal *Arctocephalus gazella*. Mammal Rev. 8:67-73.
1979. Fur seals *Arctocephalus tropicalis* and *A. gazella* crossing the Antarctic convergence at South Georgia. Mammalia 43:93-98.
1979. Growth in the Antarctic fur seal *Arctocephalus gazella*. J. Zool. 187: 1-20.
PEARSE, R. J.
1979. Distribution and conservation of the Australian fur seal in Tasmania. Victorian Nat. 96:48-53.

PIERSON, M.
1978. A study of the population dynamics and breeding behavior of the Guadalupe fur seal, *Arctocephalus townsendi*. Ph.D. thesis, Univ. Calif., Santa Cruz, 110 p.
PONCE de LEON, A.
1983. Aspectos de la reproduccion, crecimiento intrauterino y desarrollo postnatal del lobo de dos sudamericano, *Arctocephalus australis* (Zimmermann, 1783), en islas de la Republica Oriental del Uruguay. Tesis para optar a la Licenciatura, Universidad de la Republica, 163 p.
POPOV, L. A., and V. I. KRYLOV.
1977. [Kerguelen seals on King George Island.] Inf. Byull. Sov. Antarkt. Eksped. 96:66-71. (In Russian.)
REBELO, A. G.
1984. Cape fur seal *Arctocephalus pusillus* kills jackass penguin *Spheniscus demersus* on land. Cormorant 12:111-112.
RONALD, K., P. J. HEALEY, J. DOUGAN, L. J. SELLEY, and L. DUNN.
1983. An annotated bibliography on the Pinnipedia. Supplement 1. Int. Counc. Explor. Sea, Copenhagen, 346 p.
ROPPEL, A. Y.
1984. Management of northern fur seals on the Pribilof Islands, Alaska, 1786-1981. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 4, 26 p.
ROUX, J.-P.
1982. L'otarie d'Amsterdam. Actes VI[e] Colloq. Mammal., La Rochelle, p. 75-79.
ROUX, J.-P., and A. D. HES.
1984. The seasonal haul-out cycle of the fur seal *Arctocephalus tropicalis* (Gray, 1872) on Amsterdam Island. Mammalia 48:377-389.
RUSS, R.
1980. New Zealand sea lion, sea elephant, and fur seal census and habitat survey, Campbell Island group. *In* Preliminary reports of the Campbell Island Expedition 1975-76, p. 124-125. Dep. Lands and Survey, Wellington, N.Z.
SCHEFFER, V. B., C. H. FISCUS, and E. I. TODD.
1984. History of scientific study and management of the Alaskan fur seal, *Callorhinus ursinus*, 1786-1964. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF 780, 70 p.
SCHUERHOLZ, G., and G. MANN.
1977. Comments on the population of the Juan Fernandez fur seal (*Arctocephalus philippii*). Trans. 13th Int. Congr. Game Biologists, p. 290-301.
SCHUSTERMAN, R. J., and P. W. B. MOORE.
1978. Underwater audiogram of the northern fur seal, *Callorhinus ursinus*. J. Acoust. Soc. Am. 64:S87.
SHAUGHNESSY, P. D.
1979. Cape (South African) fur seal. *In* Mammals in the seas, p. 37-40. FAO Fish. Ser. 5, Vol. II.
1980. Entanglement of Cape fur seals with man-made objects. Mar. Pollut. Bull. 11:332-336.
1980. Influence of Cape fur seals on jackass penguin numbers at Sinclair Island. S. Afr. J. Wildl. Res. 10:18-21.
1981. Geographical variation in the vitamin A content of livers of adult male Cape fur seals *Arctocephalus pusillus* 1941-1949. Fish. Bull. S. Afr. 14: 123-129.
1982. The status of seals in South Africa and Namibia. *In* Mammals in the seas, p. 383-410. FAO Fish. Ser. 5, Vol. IV.
1982. The status of the Amsterdam Island fur seal. *In* Mammals in the seas, p. 411-421. FAO Fish. Ser. 5, Vol. IV.
1985. Interactions between fisheries and Cape fur seals in southern Africa. *In* Beddington, J. R., R. J. H. Beverton, and D. M. Lavigne (eds.), Marine mammals and fisheries, p. 119-134. George Allen and Unwin, Lond.
SHAUGHNESSY, P. D., and P. B. BEST.
1982. A discrete population model for the South African fur seal, *Arctocephalus pusillus pusillus*. *In* Mammals in the seas, p. 163-176. FAO Fish. Ser. 5, Vol. IV.
SHAUGHNESSY, P. D., and H. R. BURTON.
1986. Fur seals *Arctocephalus* spp. at Mawson Station, Antarctica, and in the Southern Ocean. Polar Rec. 23:79-81.
SHAUGHNESSY, P. D., and P. CHAPMAN.
1984. Commensal Cape fur seals in Cape Town docks. S. Afr. J. Mar. Sci. 2:81-91.
SHAUGHNESSY, P. D., and A. I. L. PAYNE.
1979. Incidental mortality of Cape fur seals during trawl fishing activities in South African waters. Fish. Bull. S. Afr. 12:20-25.
SHAUGHNESSY, P. D., and G. J. ROSS.
1980. Records of the sub-Antarctic fur seal (*Arctocephalus tropicalis*) from South Africa with notes on its biology and some observations of captive animals. Ann. S. Afr. Mus. 82:71-89.
SHAUGHNESSY, P. D., A. SEMMELINK, J. COOPER, and P. G. H. FROST.
1981. Attempts to develop acoustic methods of keeping Cape fur seals *Arctocephalus pusillus* from fishing nets. Biol. Conserv. 21:141-158.
SMITH, T., and T. POLACHECK.
1981. Reexamination of the life table for northern fur seals with implications about population regulatory mechanisms. *In* Fowler, C. W., and T. D. Smith (eds.), Dynamics of large mammal populations, p. 99-120. Wiley, New York.
SOBOLEVSKII, E. I.
1984. [A phenetic study of population structure of northern fur seal *Callorhinus ursinus* (Pinnipedia, Otariidae).] Zool. Zh. 63:1705-1712. (In Russian.)
SPOTTE, S.
1980. Acclimation of adult northern fur seals, *Callorhinus ursinus*, to captivity. Cetology 36:1-8.
1982. The incidence of twins in pinnipeds. Can. J. Zool. 60:2226-2233.
SPOTTE, S., and G. ADAMS.
1979. Note on the food intake of captive adult male northern fur seals (*Callorhinus ursinus*). Aquat. Mamm. 3:65-67.
1981. Feeding rate of captive adult female northern fur seals, *Callorhinus ursinus*. Fish. Bull., U.S. 79:182-184.
1981. Photoperiod and reproduction in captive female northern fur seals. Mammal Rev. 11:31-36.
STEIN, J. L., and K. MILLER.
1986. Birth of a northern fur seal on the mainland California coast. Calif. Fish Game 72:179-181.
STROUD, R. K., C. H. FISCUS, and H. KAJIMURA.
1981. Food of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, Dall's porpoise, *Phocoenoides dalli* and northern fur seal, *Callorhinus ursinus*, off California and Washington. Fish. Bull., U.S. 78:951-959.
SWARTZMAN, G. L.
1984. Factors bearing on the present status and future of the eastern Bering Sea fur seal population with special emphasis on the effect of terminating the subadult male harvest on St. Paul Island. U.S. Mar. Mamm. Comm. Rep. MMC-83/03, 77 p.
SWARTZMAN, G., and R. HAAR.
1980. Exploring interactions between fur seal populations and fisheries in the Bering Sea. U.S. Mar. Mamm. Comm. Rep. MMC-80/01, 60 p.
SWARTZMAN, G. L., and R. T. HAAR.
1983. Interactions between fur seal populations and fisheries in the Bering Sea. Fish. Bull., U.S. 81:121-132.
1985. Interactions between fur seal populations and fisheries in the Bering Sea. *In* Beddington, J. R., R. J. H. Beverton, and D. M. Lavigne (eds.), Marine mammals and fisheries, p. 62-93. George Allen and Unwin, Lond.
TAKEMURA, A., K. YOSHIDA, and N. BABA.
1983. [Distinction of individual northern fur seal pups, *Callorhinus ursinus*, through their call.] Bull. Fac. Fish., Nagasaki Univ. 54:29-34. (In Japanese.)
TAMIYA, T., S. M. ARAI, T. TSUCHIYA, and J. J. MATSUMOTO.
1977. Fractionation of ATPase accelerating peptides from fur seal muscle hydrolysate. Bull. Jpn. Soc. Sci. Fish. 43:869-876.
TAMIYA, T., M. YOSHIDA, T. TSUCHIYA, M. TANAKA, M. KIKUNO, and J. J. MATSUMOTO.
1977. Isolation of ATPase accelerating peptides from fur seal muscle hydrolysate. Bull. Jpn. Soc. Sci. Fish. 43:709-715.
TAYLOR, R. H.
1982. New Zealand fur seals at the Bounty Islands. N.Z. J. Mar. Freshw. Res. 16:1-9.
THURMAN, G. D., S. J. T. DOWNES, and S. BARROW.
1982. Anaesthetization of a Cape fur seal (*Arctocephalus pusillus*) for the treatment of achronic eye infection and amputation of a metatarsal bone. J. S. Afr. Vet. Assoc. 53:255-257.
TOLLU, B.
1981. Le jeu chez les otaries à fourrure. J. Psychologie, Nos 2-3, 215-224.
1982. Les communications chez les otaries à fourrure. J. Psychologie 1:99-124.
TORRES, D.
[no date]. First census of the Juan Fernandez fur seal *Arctocephalus philippii* (Peters) during the breeding season, 1978-1979. Natl. Geogr. Soc. Res. Rep. 18:733-743.
1981. Aumenta o disminuye la poblacion del lobo fino Antartico, *Arctocephalus gazella* (Peters), en las islas Shetland del Sur? Bol. Antart. Chileno 1(1):11-15.
TORRES, D., and A. AGUAYO.
1984. Presence of *Arctocephalus tropicalis* (Gray 1872) at the Juan Fernandez Archipelago. Chile. Acta Zool. Fenn. 172:133-134.
TORRES, D., C. GUERRA, and J. C. CARDENAS.
1984. Primeros registros de *Arctocephalus gazella* y nuevos hallazgos de *Arctocephalus tropicalis* y *Leptonychotes weddelli* en el archipelago de Juan Fernandez. Ser. Cient. Inst. Antart. Chileno 31:115-148.

TORRES, D., C. GUERRA, and M. SALLABERRY.
1983. El lobo fino del sur, *Arctocephalus australis*, en el norte de Chile. Bol. Antart. Chileno 3(1):23-24.
TRILLMICH, F.
1979. Galapagos sea lions and fur seals. Noticias de Galapagos 29:8-14.
1981. Mutual mother-pup recognition in Galapagos fur seals and sea lions: cues used and functional significance. Behaviour 78:21-42.
1983. Ketamine xylazine combination for the immobilization of Galapagos sea lions and fur seals. Vet. Rec. 112:279-280.
1984. The natural history of the Galapagos fur seal, *Arctocephalus galapagoensis*, Heller. *In* Perry, R. (ed.), Key environments: Galapagos, p. 215-223. Pergamon Press, Oxford.
1985. Effects of the 1982/83 El Niño on Galapagos fur seals and sea lions. Noticias de Galapagos 42:22-23.
1986. Maternal investment and sex-allocation in the Galapagos fur seal, *Arctocephalus galapagoensis*. Behav. Ecol. Sociobiol. 19:157-164.
1986. Attendance behavior of Galapagos fur seals. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur seals. Maternal strategies on land and at sea, p. 168-186. Princeton Univ. Press, Princeton.
TRILLMICH, F., G. L. KOOYMAN, P. MAJLUF, and M. SANCHEZ-GRIÑAN.
1986. Attendance and diving behavior of South American fur seals during El Niño in 1983. *In* Gentry, R. L., and G. L. Kooyman (eds.), Fur seals. Maternal strategies on land and at sea, p. 153-167. Princeton Univ. Press, Princeton.
TRILLMICH, F., and D. LIMBERGER.
1985. Drastic effects of El Niño on Galapagos pinnipeds. Oecologia (Berl.) 67:12-22.
TRILLMICH, F., and P. MAJLUF.
1981. First observations on colony structure, behavior and vocal repertoire of the South American fur seal (*Arctocephalus australis* Zimmermann, 1783) in Peru. Z. Saugetierkd. 46:310-22.
TRILLMICH, F., and W. MOHREN.
1981. Effects of lunar cycle on the Galapagos fur seal, *Arctocephalus galapagoensis*. Oecologia (Berl.) 48:85-92.
TRITES, A. W.
1984. Population dynamics of the Pribilof Islands northern Pacific fur seal (*Callorhinus ursinus*). M.Sc. thesis, Univ. British Columbia, 123 p.
VAZ-FERREIRA, R.
1979. South American fur seal. *In* Mammals in the seas, p. 34-36. FAO Fish. Ser. 5, Vol. II.
1980. Aspectos eto-ecologicos, explotacion y conservacion de algunos Otariidos. I Reunion Iberoamer. Zool. Vert., La Rabida 1977, p. 263-282.
1982. *Arctocephalus australis* Zimmermann, South American fur seal. *In* Mammals in the seas, p. 497-508. FAO Fish. Ser. 5, Vol. IV.
VAZ-FERREIRA, R., and S. VALLEJO.
1981. Algunos aspectos del comportamiento de *Arctocephalus australis* (Zimmerman) lobo de dos pelos de Sudamerican (Pinnipedia - Otariidae) en el Uruguay. Symposia, VI Jornadas Argentinas de Zoologia, p. 223-236.
VAZ-FERREIRA, R., S. VALLEJO, F. ACHAVAL, A. MELGAREJO, and M. MENEGHEL.
1981. Parto y comportamiento perinatal en *Arctocephalus australis* (Zimmermann), lobo de dos pelos de Sudamerica (Pinnipedia: Otariidae). Resumenes y Comun. de las Jornadas de Cienc. Nat. 2:63-64.
1981. Comportamiento de bano postnatal y otras interacciones materno-filiales en *Arctocephalus australis*, lobo de dos pelos de Sudamerica. Resumens y Comun. de las Jornadas de Cienc. Nat. 2:64-65.
VLADIMIROV, V. A.
1978. [The population status of the stock of northern fur seals (*Callorhinus ursinus curilensis*) from Robben Island.] Zool. Zh. 57:1239-1249. (In Russian.)
1980. [Elementary groups of northern fur seals.] *In* Zemskii, V. A. (ed.), Morskie mlekopitayushchie. Sbornik nauchnykh trudov, p. 61-66. VNIRO, Moscow. (In Russian.)
1980. [On the problem of intravital diagnostics of natural mortality of northern fur seals.] *In* Zemskii, V. A. (ed.), Morskie mlekopitayushchie. Sbornik nauchnykh trudov, p. 58-61. VNIRO, Moscow. (In Russian.)
1983. [On the reproductive biology of the northern fur seal females on the Uril rookery of Medyni Island.] Byull. Mosk. Ova Ispyt. Prir. Otd. Biol. 88(4):52-61. (In Russian.)
1985. [Effect of female age composition on the offspring abundance in northern fur seal.] Byull. Mosk. Ova Ispyt. Prir. Otd. Biol. 90(2):23-26. (In Russian.)
WALDORF, A., and N. A. VEDROS.
1978. Northern fur seal, *Callorhinus ursinus*, the skin and fatty acids as a natural barrier to fungal penetration. Aquat. Mamm. 6(3):77-89.
1979. Fatty acid content of depot fat in the northern fur seal (*Callorhinus ursinus*). J. Wildl. Dis. 15:573-577.
WARNEKE, R.
1979. Australian fur seal. *In* Mammals in the seas, p. 41-44. FAO Fish. Ser. 5, Vol. II.
WARNEKE, R. M., and P. D. SHAUGHNESSY.
1985. *Arctocephalus pusillus*, the South African and Australian fur seal: taxonomy, evolution, biogeography, and life history. *In* Ling, J. K., and M. M. Bryden (eds.), Studies of sea mammals in south latitudes, p. 153-177. South Australian Museum, Adelaide.
WELLS, R. M. G.
1978. Observations on the haematology and oxygen transport of the New Zealand fur seal, *Arctocephalus forsteri*. N.Z. J. Zool. 5:421-424.
WILSON, G. J.
1975. Report on the distribution and abundance of the New Zealand fur seal, *Arctocephalus forsteri*, at the Auckland Islands, 1972-73. *In* Yaldwyn, J. D. (ed.), Preliminary results of the Auckland Islands Expedition 1972-1973, p. 183-196. Dep. Lands and Survey, Wellington, N.Z.
1981. Distribution and abundance of the New Zealand fur seal, *Arctocephalus forsteri*. Occas. Publ. 20, N.Z. Minist. Agric. Fish., Fish. Res. Div., 40 p.
1981? New Zealand fur seal. Canterbury Environ. J. 7:9-11.
YORK, A. E.
1983. Average age at first reproduction of the northern fur seal (*Callorhinus ursinus*). Can. J. Fish. Aquat. Sci. 40:121-127.
YORK, A. E., and J. R. HARTLEY.
1981. Pup production following harvest of female northern fur seals. Can. J. Fish. Aquat. Sci. 38:84-90.
YOSHIDA, K.
1982. Study for reproductive mechanism of fur seal (*Callorhinus ursinus*) of Asian origin. Bull. Far Seas Fish. Res. Lab. 20:1-36.
YOSHIDA, K., and N. BABA.
1982. A study of behavior and ecology of female fur seals on a breeding island by radio wave telemetry and visual observation. Bull. Far Seas Fish. Res. Lab. 20:37-63.
YOSHIDA, K., N. BABA, M. OYA, and K. MIZUE.
1977. On the formation and regression of corpus luteum in the northern fur seal ovaries. Sci. Rep. Whales Res. Inst. 29:121-128.
1978. Seasonal changes in the ovary of the northern fur seal. Bull. Far Seas Fish. Res. Lab. 16:93-101.
YOUNG, O. R.
1981. The political economy of the northern fur seal. Polar Rec. 20:407-416.

NOAA TECHNICAL REPORT NMFS

Guidelines for Contributors

FORM OF MANUSCRIPT

Authors are encouraged to retain manuscripts on word processing storage media, such as diskettes, floppy disks, cassette or magnetic tapes, and submit a hard copy run from the storage media. Hardcopy should be typed double-spaced on white bond paper in the following sequence:

Title page
Contents
Abstract
Text
Acknowledgments
Citations
Text footnotes
Appendix
Tables
Figure Legends
Figures

CONTENTS OF MANUSCRIPT

Contents. Contains all text headings with page numbers omitted.

Abstract. Not to exceed one double-spaced typed page. Should include a sentence or two explaining to the general reader why the research was undertaken and why the results should be viewed as important. Abstract should convey the main point of the paper and outline the results or conclusions. Footnotes and references do not belong in the abstract.

Text. A brief introduction should portray the broad significance of the paper. The entire text should be intelligible to readers from different disciplines. All technical terms should be defined. Follow the *U.S. Government Printing Office Style Manual*, 1984 edition.

Fishery nomenclature follows the American Fisheries Society Special Publication No. 12, *A List of Common and Scientific Names of Fishes from the United States and Canada*, 4th edition, 1980.

Abbreviations and symbols. Define all symbols, abbreviations, and acronyms. Define all symbols in equations and formulas. Abbreviate units of measure only when used with numerals or in tables and figures where there is lack of space. Periods are rarely used except for et al., vs., e.g., i.e., etc.

Measurements should be expressed in metric units. Other equivalent units may be given in parentheses.

Text footnotes. Type on a separate sheet from the text. Footnotes are not used for reference material or personal communications, but rather to explain or define terms in the text and for contribution numbers.

Personal communications are noted in parentheses in the text (name, affiliation, brief address including zip code, month and year).

Citations. All written sources should be listed in the Citations section, including unpublished and processed material. In text, cite as Smith and Jones (1977) or (Smith and Jones 1977); if more than one citation, list chronologically (Smith 1936; Jones 1975; Doe 1977). All sources cited in the text should be listed alphabetically by the senior authors' surname under the heading CITATIONS. Abbreviations of periodicals and serials should conform to the Biosis Data Base™. The author is responsible for the accuracy of all citations.

Acknowledgments. Gather all acknowledgments into a brief statement at the end of the text. Give credit only for exceptional contributions and not to those whose contributions are part of their normal duties.

Tables. Tables should supplement, not duplicate, the text. Each table should appear on a separate page, and be numbered consecutively. Headings should be short but amply descriptive so that the reader need not refer to the text. For values less than 1, zeros should precede all decimal points. Give each column a heading with units of measure indicated in parentheses. Do not change the unit of measure within a column. Table footnotes should be numbered consecutively in Arabic numerals across the page from left to right and down; to avoid confusion with exponents, place them to the left of numerals, e.g., $^{3}10$. All tables should be cited consecutively in the text and their placement, where first mentioned, indicated in the left-hand margin of the manuscript page. Lengthy tables that are typed in the proper format and are clean and legible can be used camera-ready.

Figures. Photographs and line drawings should be of professional quality—clear and concise—and reducible to 42 picas for full-page width or to 20 picas for a single-column width, and a maximum of 57 picas high. All illustrations must be proportioned so that they are legible when reduced to fit the page format. Line weight and lettering should be sharp and even. Lettering on graphs should be upper and lower case, and vertical lettering should be avoided as much as possible (except for vertical, y, axis). For values less than 1, zeros should precede all decimal points. Reproductions of line art work are accepted in the form of photographic prints from negatives or photomechanical transfer. Halftones should be sharply focused with good contrast. Micron rules should be inserted on electron micrographs, even when magnification is included in the figure legend. There should be good distinction between identifying letters (preferably press-on) and background of photograph. All figures should be cited consecutively in the text and their placement, where first mentioned, indicated in the left-hand margin of the manuscript page. Each figure should be labeled in pencil on the back. DO NOT SEND original or photographic prints of figures to the Scientific Editor; they will be requested when the manuscript is accepted for publication.

Copyright. Government publications are in the public domain, i.e., they are not protected by copyright.

SUBMISSION OF MANUSCRIPTS

Send original hardcopy and two duplicated copies of the manuscript to:

Dr. Andrew E. Dizon, Scientific Editor
NOAA Technical Reports NMFS
Southwest Fisheries Center
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, CA 92038-0271

Indicate whether word processing storage media are available, but do not forward disks until requested by Scientific Editor or Scientific Publications office.

Copies of published reports. For single monographs, the senior author will be provided with 50 copies free of charge and 50 to his or her organization. For collections of papers, each senior author will receive 50 separates and one cover, and his or her organization will receive the same. Additional copies may be purchased in lots of 100.

ADDITIONAL INFORMATION

Questions regarding editorial policy and procedures may be forwarded to:

Nancy Peacock, Managing Editor
NOAA Technical Reports NMFS
National Marine Fisheries Service, NOAA
Scientific Publications Office
Bin C15700
Seattle, WA 98115

UNITED STATES
DEPARTMENT OF COMMERCE
NATIONAL OCEANIC AND ATMOSPHERIC
ADMINISTRATION
NATIONAL MARINE FISHERIES SERVICE
SCIENTIFIC PUBLICATIONS OFFICE
BIN C15700
SEATTLE, WA 98115
OFFICIAL BUSINESS

Penalty for Private Use, $300

BULK RATE
POSTAGE & FEES PAID
U.S. Department of Commerce
Permit No. G-19

NOAA SCIENTIFIC AND TECHNICAL PUBLICATIONS

The National Oceanic and Atmospheric Administration was established as part of the Department of Commerce on October 13, 1970. The mission responsibilities of NOAA are to assess the socioeconomic impact of natural and technological changes in the environment and to monitor and predict the state of the solid Earth, the oceans and their living resources, the atmosphere, and the space environment of the Earth.

The major components of NOAA regularly produce various types of scientific and technical information in the following kinds of publications:

PROFESSIONAL PAPERS—Important definitive research results, major techniques, and special investigations.

CONTRACT AND GRANT REPORTS—Reports prepared by contractors or grantees under NOAA sponsorship.

ATLAS—Presentation of analyzed data generally in the form of maps showing distribution of rainfall, chemical and physical conditions of oceans and atmosphere, distribution of fishes and marine mammals, ionospheric conditions, etc.

TECHNICAL SERVICE PUBLICATIONS—Reports containing data, observations, instructions, etc. A partial listing includes data serials; predictions and outlook periodicals; technical manuals, training papers, planning reports, and information serials; and miscellaneous technical publications.

TECHNICAL REPORTS—Journal quality with extensive details, mathematical developments, or data listings.

TECHNICAL MEMORANDUMS—Reports of preliminary, partial, or negative research or technology results, interim instructions, and the like.

Information on availability of NOAA publications can be obtained from:

U.S. Department of Commerce
National Technical Information Service
5285 Port Royal Road
Springfield, VA 22161